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Impacts of forest floor disturbance on vegetation and nutrient dynamics in clearcut and partial cut stands

By

Brent Regan Frey ©

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Impacts of forest floor disturbance on vegetation and nutrient dynamics in clearcut and partial cut stands by Brent Regan Frey in partial fulfillment of the requirements for the degree of Master of Science in Forest Biology and Management.

Dedication

to my sister Wendy
and her unyielding spirit and good humour in the face of adversity

Abstract

This thesis evaluated the effects of harvesting (clearcut vs. partial cut) and forest floor disturbance (burn, mix, mound and scalp) on vegetation and nutrient dynamics in white spruce stands in the boreal mixedwood of Alberta. There tended to be higher Mg and Ca availability, and greater *Populus* spp. density and cover in the clearcut. Otherwise, impacts were associated with forest floor disturbance. Nutrient availability was generally increased by forest floor treatments, depending on the nutrient. Net N mineralization was highest in the inverted forest floor of the mound, and lowest in the mix. Burning increased cover of *E. angustifolium*, scalping promoted root suckering by *Populus* spp., while mixing and mounding limited vegetation establishment. In a separate study, *E. angustifolium* sprouts were cut and fertilized with N to determine a mechanism for increased sprouting following fire. Destruction of the dominant shoot stimulated sprouting, while N addition only stimulated higher aboveground biomass.

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Chapter 1. Responses of nutrients and vegetation to forest floor disturbance and canopy removal.

Introduction

In the Canadian boreal forest, regeneration of white spruce in harvested stands is an important, yet challenging silvicultural objective. The typical silvicultural system for white spruce regeneration is clearcut harvest followed by site preparation and planting of tree seedlings. Successful seedling establishment is highly dependent upon microsite conditions; vegetation competition, soil temperature and nutrient availability all significantly affect white spruce growth (Brand and Janas 1987, Delong et al. 1997).

The disturbance created by clearcutting alters the environmental conditions substantially, increasing light availability, soil temperature, soil moisture and nutrient availability. These dramatic increases in resource availability favour vigorous establishment by early successional plant species, which in turn can pose significant competitive problems for white spruce regeneration (Lieffers et al. 1993). Clearcutting thus necessitates further interventions to ensure white spruce establishment. Mechanical site preparation treatments such as blading, disc trenching, mounding and mixing are typically used to create more favourable microsites for white spruce growth (Lieffers and Beck 1994). Herbicide use is common for vegetation control and prescribed burning may also be used for site preparation. While improving regeneration success, these measures may be costly, and/or viewed as unacceptable to the public. Furthermore, these measures add another level of disturbance to the system, with consequences for successional development, long-term productivity and ground water contamination.

Considering the subsequent interventions required within a clearcut system, it is surprising that alternative systems have received little attention. Many studies have examined the impacts of disturbance at the canopy level, but the focus has been primarily on the impacts of clearcutting. Forest floor level disturbances such as fire and mechanical site preparation have received considerable attention as well. Alternatives to clearcutting, such as partial cutting have received significantly less attention, despite the evidence of the beneficial impacts that partial canopy retention might convey in terms of

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vegetation control and tree seedling growth (Lieffers et al. 1993, Man and Lieffers 1999). Only a few studies have evaluated the interactions between canopy disturbance and forest floor disturbance (e.g. Burgess and Wetzel 2000, Holgen and Hånell 2000, Man and Lieffers 1999, Vitousek et al. 1992). A more integrated approach will consider not only treatments at the forest floor level but also variable levels of canopy removal.

The following section reviews the responses of vegetation and nutrients to disturbance at the canopy or forest floor level. The primary focus at the canopy level will be on forest harvesting – either clearcut or partial cut – as much of the literature relates to these types of disturbance. Disturbance at the forest floor level will focus on impacts of mechanical site preparation (MSP) treatments, as they constitute the most important management disturbance to the forest floor, and on fire effects, since consumption of the forest floor by burning creates the natural substrate for regeneration in this system.

Canopy Disturbance

The partial or complete removal of the forest canopy modifies environmental conditions at the forest floor substantially. Canopy loss results in increased wind speeds and reduced humidity, as well as increased insolation and reduced evapotranspiration which drive increased soil temperature and moisture (Man and Lieffers 1999). The degree to which these environmental conditions are altered will be a function of the extent of canopy loss. The impacts of canopy disturbance on vegetation and nutrient dynamics are discussed below.

Canopy disturbance: impacts on nutrient dynamics

The impact of clearcutting on nutrient dynamics has been rigorously evaluated; nitrogen availability generally increases after clearcutting (Matson and Vitousek 1981, Binkley 1984, Smethurst and Nambiar 1990a, Kim et al. 1995). This trend is reasonable given reduced uptake of nutrients following tree removal. Increased nitrogen availability in clearcuts is also attributed to increased rates of decomposition. As soil moisture and temperature are strongly correlated with microbial activity (Bunnell et al. 1976), increased soil moisture and temperature conditions in clearcuts should favour higher rates of decomposition (Kimmins 1997). Evidence for increased decomposition rates

following clearcutting, however, has been mixed (Prescott 1997). This ambiguity may relate to the fact that different studies examined different layers of the forest floor. Decomposition rates within the forest floor have been shown to increase or decrease following canopy removal, depending upon the particular horizon being evaluated (Binkley 1984), a response that may be a function of the resulting moisture conditions in a particular forest floor layer following disturbance (Yin et al. 1989). Though soil moisture generally increases following cutting, the exposed surface layers may dry out, depending upon regional climate (Yin et al. 1989). Surface drying may result in diminished rates of decomposition.

Higher levels of N mineralization facilitate nitrification, typically resulting in high levels of NO_3^- following clearcutting (Vitousek et al. 1982, Prescott 1997). Nitrate is highly mobile and susceptible to leaching, potentially resulting in significant losses of N from the system following disturbance (Vitousek et al. 1982). Moreover, the nitrification process can lead to soil acidification due to the displacement of base cations (Nambu et al. 1994). A number of studies, summarized by Kimmins (1997), have shown that the degree of N loss following disturbance is inversely related to the recovery of vegetation.

There is substantially less information relating to impacts of partial canopy loss on nutrient dynamics. The few studies that exist suggest that partial canopy removal moderates nutrient loss relative to clearcuts, e.g. in an oak forest partial canopy removal resulted in increased N mineralization, although not as high as in the clearcut (Kim et al. 1995). However, Prescott (1997) in a comparative study of several levels of canopy removal found increased N in the clearcuts, but no significant difference between partial cut and uncut stands. Moreover, partial cut white pine stands in the third growing season following thinning did not show any differences in N availability compared to uncut stands (Burgess and Wetzel 2000). Evidence from studies of natural gaps suggests that N availability increases in gaps (Paré et al. 1993) although higher availability may be spatially confined to the central area of the gap where root abundance and uptake are at their minimum (Palik et al. 1997). Evidence from the above studies suggests that nutrient availability may not vary directly with the level of canopy removal, the differences may not be large enough to detect, and/or the increase in availability may be short-lived owing to uptake by the remaining trees. As a consequence, it is not clear

what effect partial-canopy removal will have on nutrient availability in a particular situation.

Canopy disturbance: impacts on vegetation dynamics

The response of vegetation to canopy removal is likely driven by increases in light, temperature, moisture and nutrient availability. Vegetation response to canopy disturbance will be determined by both the availability of viable propagules (seedbank, budbank) within the site as well as by seed dispersal into the disturbed area. Many early successional species in the boreal forest, such as *Calamagrostis canadensis*, are clonal, may persist in the understory of closed canopy stands, and are capable of rapid site colonization through rhizome growth once the canopy is removed (Ahlgren 1960, Lieffers et al. 1993). Stand developmental stage related to crown closure will to a large degree affect the distribution and abundance of competitor species in the understory, and thereby determine how vigorously they can respond to stand removal (Smidt and Puettmann 1999).

The degree of canopy removal will determine the increase in light availability as well as increases in moisture, temperature and nutrient availability, and thus will strongly affect which plants respond, and the vigour of their response. After complete canopy removal, vigorous growth of clonal vegetation is widely observed in boreal mixedwoods (Lieffers et al. 1993, Mallik et al. 1997). *Calmagrostis canadensis* and *Epilobium angustifolium* are two of the most common early successional species that colonize sites following the complete loss of canopy either by clearcutting or by fire. *Calamagrostis canadensis* commonly colonizes clearcut sites through rhizome growth, creating problems for tree seedling establishment (Eis 1981, Lieffers et al. 1993). *Calamagrostis canadensis* is a prolific seed producer and may seed into clearcut blocks (Lieffers et al. 1993). *Epilobium angustifolium* is also a prolific seed producer and is known to rapidly colonize burned stands by seed (Dyrness and Norum 1983). Aspen regeneration from root suckers is also common on mixedwood sites in the boreal forest after canopy disturbance (Lavertu et al. 1994).

Little information is available on the impacts of partial canopy removal on understory vegetation. It is thought that the intermediate light levels resulting under

partial canopy removal will limit the vigour and expansion of early successional species relative to complete canopy removal (Lieffers et al. 1993, Lieffers et al. 1999). Comparisons of natural stands with different light levels suggest that early successional species are reduced in vigour and abundance in lower light conditions (Lieffers and Stadt 1994). Conversely, retention of later successional species appears to be enhanced under shelterwood conditions relative to complete canopy removal (Hannerz and Hånell 1997).

Forest Floor Disturbance

Forest floor disturbance in the boreal forest is attributable to natural disturbances (primarily wildfire but also windthrow) and from management activities through harvesting and mechanical site preparation (MSP). They differ substantially in their impacts. MSP treatments such as blading may manipulate the forest floor in ways physically similar to burns by partial or complete removal of the forest floor to expose mineral soil. However, effects of MSP treatments differ substantially from that of fire, primarily through the redistribution and fragmentation of the forest floor and mineral soil. Mixing treatments, such as done by a Meri-crusher, fragment the forest floor material and mix it with mineral soil. Mounding treatments invert the soil, burying two layers of forest floor under a mineral cap. Discing and trenching treatments redistribute organic matter and mineral soil in a way somewhat analogous to plowing an agricultural field, resulting in a raised furrow and a trench.

Fire, in contrast, results in a variable degree of forest floor removal, dependent upon moisture and fire intensity. Fire disturbance moves from the surface downwards, creating a blackened surface, and there can be significant variation in forest floor consumption within a burn. Consumption of the forest floor by fire generally results in the loss of some nutrients (e.g. N, S) to the atmosphere by volatilization, and the mineralization of other nutrients (e.g. Ca, Mg, K), consequently elevating soil pH. While burns may result in significant loss of forest floor and the exposure of mineral soil, they do not directly result in the upheaval or mixing of the forest floor, nor do they create elevated furrows or mounds. Consequently, the main differences between mechanical site preparation and fire are the degree of fragmentation to the forest floor and its associated vegetative structures, the degree of spatial rearrangement of soil horizons, the

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surface albedo, the flux of nutrients and the degree of compaction associated with the equipment.

Forest floor disturbance: impacts on nutrient dynamics

In boreal forests, the forest floor represents the principal reservoir of nutrients (Van Cleve et al. 1983), thus disturbance at the forest floor level will potentially have significant effects on nutrient dynamics. Fire is the dominant natural disturbance to the forest floor, while mechanical site preparation is the most common ground disturbance in managed stands of western Canada. They differ in their intensity, their level of displacement of organic matter and thus in their impact. It has been noted that significant changes in soil properties, such as pH and nutrient availability, may only result when fires remove substantial amounts of forest floor (Van Cleve and Dyrness 1983). Given the range of potential disturbances to the forest floor – from wildfire to mechanical site preparation – it is difficult to generalize the responses.

Fire has several effects on the forest floor in terms of nutrient cycling. Fire consumes organic matter, volatizing C, N, S and to a lesser degree P and leaving behind cations such as Mg, K, Ca (Feller 1982). There may be an increase in available N concentrations under moderate burns, but N availability decreases in heavier burns, whereas P availability tends to increase with burn intensity (Dyrness and Norum 1983). The release of cations with organic matter consumption results in a generally observed increase in pH (Feller 1982, Dyness and Norum 1983, Bauhus et al. 1993, Pietikäinen and Fritze 1995). Both the increase in base cations and pH following fire tend to promote increased levels of nitrification (Bauhus et al. 1993). A short term reduction in microbial biomass is also noted after fire, with fungal biomass appearing to be more significantly reduced than bacteria (Pietikäinen et al. 1995). This disproportionate loss or reduction in fungal biomass following fire may have a significant negative effect on decomposition given the recalcitrant nature of boreal forest floors.

MSP treatments can also significantly alter the environment for microbial activity. Increases in microsite temperature have been observed with disk-trenching (Weber et al. 1995) and with the removal of slash (Smethhurst and Nambiar 1990b, Brand and Janas 1987). Moisture may increase or decrease following site preparation, depending

primarily upon the creation of elevated or depressional positions. However, soil moisture often decreases with site preparation (Mallik and Hu 1997), especially in exposed surface organic layers where slash is removed (Smethurst and Nambiar 1990b). As soil moisture and temperature are the primary environmental factors governing microbial activity (Bunnell et al. 1976), changes to temperature and moisture regimes accompanying site preparation can affect rates of decomposition and nutrient release. Observations of substrate decay indicate that needle litter decomposes more rapidly in disk-trenched sites resulting from elevated temperatures (Lundmark-Thelin and Johannson 1997). As well, measurements of CO_2 release in mixed plots have indicated increased microbial activity from site preparation resulting from improved soil moisture and aeration (Mallik and Hu 1997).

As a consequence of greater microbial activity, nutrient availability will in some cases increase with site preparation. Nutrient release is stimulated by disk-trenching (Lundmark-Thelin and Johannson 1997) and shear-pile-disk treatments (Vitousek et al. 1992). At the same time, however, nutrient availability will be limited largely by the extent to which the treatment suppresses vegetation establishment. As will be seen in the following section, different treatments may be very effective at controlling vegetation. Studies comparing herbicide treatments with mechanical site preparation indicate that suppression of vegetation is the most important factor affecting nutrient availability (Vitousek et al. 1992, Munson et al. 1993). Consequently, N may increase with site preparation but this may be more attributable to decreases in plant nutrient uptake than to increases in decomposition and mineralization.

Forest floor disturbance: impacts on vegetation

The type, intensity and timing of disturbance will interact with regenerative structures to determine the plant community response to disturbance. Ground level disturbance can damage or kill above ground vegetative structures, alter or remove the forest floor, and rearrange or expose propagules as well as change the seedbed substrate. Reestablishment of vegetation will be primarily a function of the depth of disturbance, the type and viability of plant propagules remaining in the soil, the extent of seed dispersal into the site from surrounding areas, and the environmental conditions in the

recently disturbed area. In order to understand the dynamics of vegetation responses to ground disturbance, it is important to assess the patterns of propagules (seed bank and bud bank) distribution and regenerative ability in the forest floor, as well as examine the types, timing and intensity of common disturbances.

Propagules

The boreal forest floor contains extensive clonal root/rhizome systems as well as a sizeable seed bank, both of which may be defined in terms of spatial distribution. Seed banks have received considerable attention and relative to the bud bank, are well studied (Schimmel and Granström 1996). The seed bank is characterized by declining seed density and species richness with increasing depth (Qi and Scarratt 1999). However, seed density is often low in the surface litter, with highest densities found below the litter layer (Rydgren et al. 1998). Much less is known about clonal systems and bud bank distribution in the boreal forest (Schimmel and Granström 1996, Mallik et al. 1997). Wide variation in clonal size, foraging and allocation of biomass belowground, have been seen amongst different species in other ecosystems (e.g. Lezberg et al. 1999). Root and rhizome systems of boreal clonal species may be more or less extensive, likely dependent upon both canopy openness and the species (Lieffers and Stadt 1994, Broderick 1990). The depth of clonal systems also varies among species, with some species developing rhizome and root networks in the mineral soil, while others may be more confined to the organic horizon. The rhizomes of fireweed, for example, are typically found 2 to 8 cm deep into the mineral soil (Moss 1936, McLean 1968). In contrast, *Calamagrostis canadensis* rhizomes tends to be found in the organic horizons or organic-mineral interface (Lieffers et al. 1993).

Disturbance and vegetation response

Numerous studies have examined the impacts of forest floor disturbance on plant responses in the boreal forest. Studies have investigated plant community and diversity response (Peltzer et al. 2000, Driscoll et al. 1998), as well as species-specific responses (e.g. Haeussler et al. 1999) to different disturbance types. A species may be enhanced by one treatment and diminished by another, e.g. V-blade and brush rake site preparation

were shown to increase the amount of fireweed, while disking did not (Jobidon 1990). Some species are very sensitive to forest floor disturbance, as for example, velvet-leaved blueberry which is reduced substantially by site disturbance (Haeussler et al. 1999). Indeed, disturbance intensity has a significant role in determining the community-level response vis-à-vis the promotion or reduction of individual plant species (Peltzer et al. 2000).

Given the large variation in propagule types and in disturbance intensity and type, a wide variation in vegetation response is expected. Many of the ground disturbance studies, such as the ones noted above, have measured the general plant community response and highlighted the effects on selected species. However, a mechanistic understanding of species specific responses to disturbance is generally lacking (Mallik et al. 1997). As a consequence, reference must be made to the few more rigorously studied boreal species such *as Calamagrostis canadensis, Epilobium angustifolium, Populus tremuloides* as well as some other northern forest plant species (e.g. *Gaultheria shallon, Rubus parviflorus*) for characterizing patterns of plant response to disturbance in the boreal forest.

First, disturbance may result in damage to, or destruction of, shoots and or below ground propagules. Shoot damage has been shown to release axillary buds, resulting in increased shoot production (Powelson and Lieffers 1991). Cutting of fireweed stems stimulates stembases to produce more shoots and rhizomes (Coates and Haeussler 1986). Consequently, ground disturbance may initiate increased vegetative regeneration through disturbance to aboveground shoots. Impacts of fire on vegetative structures and seed bank are best assessed through depth of burn (Schimmel and Granström 1996). Heat penetration is limited by the poor thermal conductivity of the forest floor and thus heat penetration lethal to plants appears to be constrained to a depth of 20-30mm (Schimmel and Granström 1996). Vegetative structures below this level will likely not be destroyed by heat.

Second, disturbance may result in the burial or exposure of regenerative organs or seeds. Site preparation such as mounding can result in burial of clonal structures. It was found that the thickness of the mineral soil cap of mounded microsites significantly affected the establishment of *Calamagrostis canadensis* (Landhäusser and Lieffers 1999).

In Quebec, removal of the forest floor in small clearcuts resulted in higher suckering of aspen compared to no forest floor removal (Lavertu et al. 1994).

Third, disturbance may result in wounding or fragmentation. Severed rhizomes will release dormancy of lateral buds (Charpentier et al 1998, Powelson and Lieffers 1991). Treatments such as mixing, which fragment root systems, could result in the release of dormant buds on rhizomes, as for example in *Calamagrostis canadensis* (Powelson and Lieffers 1991). This release of buds from dormancy is seen in a number of species, and may be an adaptation to perturbation (Charpentier et al. 1998). However, severe fragmentation may kill buds and result in poor sprouting (Powelson and Lieffers 1991).

Fourth, disturbance will modify the seed bed condition, thereby improving or diminishing the success of seedling establishment. Seed bed quality is dependent upon the amount of residual organic matter (Schimmel and Granström 1996). Forest floor litter is a poor germination substrate, but decomposed humus and mineral soil substrates promote establishment of seedlings (Rydgren et al. 1998). Thus a disturbance that removes the upper litter layers will be beneficial to seedling establishment.

Fifth, temperature has an effect on regeneration. Temperatures are higher in elevated positions above the forest floor, or where the insulating forest floor layer has been removed (Brand and Janas 1987, Smethhurst and Nambiar 1990b, Weber et al. 1995). Temperature affects vegetative reproduction of fireweed (Landhäusser and Lieffers 1994). In Quebec, removal of the forest floor in small clearcuts resulted in higher suckering of aspen compared to no forest floor removal (Lavertu et al. 1994). This response was possibly related to temperature.

Schimmel and Granström (1996) present a generalized model of how different regenerative structures are affected by variable burn intensities. They suggest that clonal regeneration will be favoured at lower levels of forest floor reduction where belowground vegetative structures are not destroyed. Establishment of seedlings on a disturbed site will, in contrast, be most favoured by high levels of forest floor reduction because the resident seed and bud bank is likely to be destroyed and because the deep burning creates a suitable seedbed. Regeneration by the seed bank will be most favoured with intermediate consumption, which reduces the forest floor and provides exposure, but does

not destroy all of the seed bank. This general model is based upon fire disturbance, but the principles may be applicable to some of the microsites created by mechanical ground disturbance.

In summary, the distribution of seeds and clonal systems in the forest floor and upper mineral soil will affect their susceptibility to being exposed, fragmented, wounded or consumed by disturbances such as fire, harvesting or mechanical site preparation. The response of plant species will be highly dependent upon their life-history or mode of regeneration (Rydgren et al. 1998). Unfortunately, the autecology of most boreal shrub and herb species is poorly understood, thus there is a clear need to know more about disturbance-related responses of specific plants to different types of disturbance in the boreal forest (Mallik et al. 1997).

Thesis Objectives

The response of vegetation and nutrients to disturbance at either the forest floor level and or the canopy level clearly involves many different factors. Given the important role that vegetation and nutrient dynamics play in determining the success of tree seedling establishment, it is critical that these dynamics be better understood. Alternative silvicultural approaches to clearcutting such as partial cutting, perhaps in conjunction with MSP, may provide improved seedling establishment through better management of vegetation and nutrient dynamics. However, these alternatives need to be evaluated to determine how they impact vegetation and nutrients.

The objective of this thesis was to assess the response of nutrients and vegetation to different types of disturbance. Specifically, this study assessed the contribution of disturbance at either the forest floor level or canopy levels as they affected changes in nutrients and vegetation. In addition, this study integrated environmental measures (temperature, moisture, light) to attempt to identify the factors driving changes in vegetation and nutrient dynamics. The short-term responses of vegetation and nutrients to the different treatments provide a basis for evaluating the potential success of planted seedlings. A further objective was to determine the mechanisms involved in increased sprouting of *E. angustifolium* following light surface burns.

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Chapter 2. Impacts of forest disturbance on nutrient and vegetation dynamics in clearcut and partial cut stands.

Introduction

In the mixed-wood boreal forest of Alberta, establishment of white spruce in harvested stands is an important, yet challenging silvicultural objective. Regeneration and growth of white spruce is highly affected by microsite conditions, especially vegetation competition, soil temperature and nutrient availability (Brand and Janas 1987, Delong et al. 1997). Vegetation competition is considered to be the most important determinant of seedling success, as it affects not only light availability but also soil temperature, availability of nutrients and moisture (Munson et al. 1993). Such species as *Epilobium angustifolium* or *Calamagrostis canadensis* establish vigorously on boreal sites following disturbances such as clearcutting (Hogg and Lieffers 1991a) or fire (Dyrness and Norum 1983) and pose significant competition problems. The growth of spruce will be highly dependent upon the control of these competitors (Thevathasan et al. 2000).

Control of competing vegetation is commonly provided through the application of herbicides, however their use is perceived negatively by the public. Consequently, alternate vegetation management strategies are sought for the successful establishment of planted white spruce. Strategies such as partial canopy retention or forest floor treatments (mechanical site preparation or prescribed burning) could be used to limit the development of competing vegetation (Lieffers et al. 1993).

Partial cut systems have received increasing attention as a means to control competing vegetation and improve seedling establishment. Silvicultural systems that retain partial canopies will limit light availability in the understory and may shade out competitors sufficiently to allow establishment of spruce seedlings (Lieffers et al. 1993). For example, both *E. angustifolium* and *C. canadensis* species are adapted to open light conditions of disturbed sites, and tend to be less vigorous and abundant under denser canopies. At 40 percent light, white spruce seedling growth is maintained, while cover and height of *C. canadensis* and *E. angustifolium* are significantly diminished (Lieffers and Stadt 1994).

Forest floor treatments provide another silvicultural option for limiting competing vegetation and improving the seedling microsite (Lieffers et al. 1993, Landhäusser and Lieffers 1999). Mechanical site preparation (MSP) treatments such as blading, disc trenching, mounding and mixing are typically used to create more favourable microsites for white spruce growth (Lieffers and Beck 1994). Prescribed burning has been utilized extensively in British Columbia to reduce slash and forest floor, thereby increasing temperature and nutrient availability and possibly reducing competition (Feller 1982).

The complete or partial removal of the canopy and or forest floor disturbance will also affect nutrient dynamics by reducing nutrient uptake and altering environmental conditions at the forest floor level. In boreal forests, the forest floor represents the principal reservoir of nutrients (Van Cleve et al. 1983), thus silvicultural treatments that impact the forest floor may significantly affect nutrient cycling and plant growth. Significant increases in forest floor nitrogen availability have been noted after clear cutting (Binkley 1984). Moreover, site preparation in harvested stands may further increase (Vitousek et al. 1992) or decrease (Munson and Timmer 1995) rates of N mineralization. In boreal forests, fire plays a dominant role in forest floor disturbance. Forest floor consumption by fire may result in increased or decreased N and P concentrations depending upon burn intensity (Dyrness and Norum 1983). Soil pH, and cation exchange capacity (CEC) generally increase under burning, although the latter may increase or decrease depending on the extent of forest floor loss (Feller 1982). Increased nutrient availability may increase leaching, and primarily benefits competitors of white spruce in the initial years after planting (Thevathasan 2000).

Mechanical site preparation or prescribed burning could be used in conjunction with different cutting systems for preparing forest sites for regeneration. The retention of a partial canopy will reduce insolation relative to complete canopy removal (clearcut) which may result in lower soil temperatures, microbial activity and mineralization rates – all possibly affecting plant response. Site preparation will also alter soil temperature and moisture, microbial activity, mineralization rates and plant reestablishment. However, the interactive effects of combined harvest and site preparation are not evident, as there has been little investigation into the use of partial cut systems with understory site preparation, especially in terms of vegetation control (Lieffers et al. 1993). Moreover,

tree removal from the 15m wide retention strips (Figure 2.1). Canopy light transmission in the PC averaged 48%.

The forest floor disturbance treatments consisted of light burn, scalp, mix and mound plots as well as an undisturbed control plot. Forest floor disturbance treatments were approximately 2m X 2m plots buffered by at least 1m from any adjacent plot, and were replicated four times in each canopy treatment replicate. Within the PC, forest floor disturbance plots were located in the central area of the retention strip (Figure 2.1) while in the CC, forest floor disturbance plots were located in the central area of the clearcut away from forest edges. Forest floor disturbance plots were located on sites determined to be uniform in microtopography, slope, soil and forest floor depth. Mechanical site preparation plots were installed in late May 1999 with an excavator using two attachments (a mounding bucket for scalp and mound treatments and a Meri-Crusher high-speed horizontal drum mulcher for the mixing treatments). The mounding treatment created inverted mineral-capped mounds of approximately 1m diameter and 15 cm deep mineral-capping (for this treatment only, four adjacent mounds created one mound plot). The scalping treatment removed the majority of the forest floor, leaving an average of 2 cm of H layer above the mineral soil. The mixing treatment fragmented and mixed the forest floor with the upper 2-3 cm of mineral soil. The burning treatment was carried out during the last week of May and first week of June using a propane torch. Burn pins placed into the plot before burning indicated that the average depth of burn was approximately 2 cm. Consumption was limited primarily to the surface litter/moss layer, thereby creating a scorched and blackened surface.

In mid-July 1999, white spruce seedlings were planted into each treatment plot. Each of the four mounds in a mound plot were planted with a seedling, while all other treatment plots were planted with five seedlings (one in each corner of the plot and one in the centre).

Environmental Measurements

Mineral and organic soil cores (each 2 cm in diameter and approximately 7 cm long) were removed from each forest floor disturbance plot in July and August 1999. Sampling was done at least four days after a rain event. Soil moisture content was

determined gravimetrically. Cores were dried for 48 hours at either 105°C (for mineral cores) or 68°C (for organic cores). Soil temperatures were assessed between 2:30 pm and 5:00 pm on clear days in June, July and August 1999. A portable digital thermometer (Universal Enterprises, Beaverton, OR) was fixed to copper-constantin thermocouples placed at depths of 5 cm and 20 cm in each plot. The June to August temperature measurements were averaged for each plot to provide an average midday temperature for each treatment.

Resin bag preparation, installation and extraction

Resin bags were made by placing 35mL of mixed-bed cation + anion type 1 IONAC NM-60 H+/OH- (16-50mesh) exchange resin (J.T. Baker, New Jersey, U.S.A.) into nylon bags. Resin bags were tied shut, and prepared following the procedure of Thiffault et al. (2000). Briefly, resin bags were completely covered in a 2N NaCl solution and were allowed to stand for one hour with occasional stirring. Resin bags were then rinsed repeatedly with deionized water, placed in a solution of 0.1N NaOH, and stirred for 1 hour. Bags were then rinsed repeatedly with deionized water, excess water was squeezed out and they were placed in sealed bags and refrigerated until field placement.

Three resin bags were placed separately within the central area of each forest floor disturbance plot in mid-June 1999, following the placement procedure of Munson and Timmer (1995). A spade was inserted at 45 degrees to create a slit in the soil, and the bags were placed flat against the soil surface in the upper 5 cm of the mineral soil (directly below the organic-mineral interface) (Figure 2.2). The spade was then removed, the soil pushed down to ensure good contact and resin bags were flagged for later retrieval. Bags were removed in October 1999.

In the lab, bags were washed thoroughly with deionized water. Each bag of resin was opened and the resin contents were extracted by shaking for 1 hour in 100mL of 2N NaCl solution. Extracts were filtered (Fisherbrand P4), the three extracts for each forest floor disturbance plot were then pooled and analyzed for ammonium (NH_4^+), nitrate (NO_3^-), and phosphorous (P) using a Technicon Autoanalyzer, and for potassium (K^+),

magnesium (Mg^{2+}) and calcium (Ca^{2+}) by atomic absorption spectrophotometry (Perkin-Elmer 503).

Field Incubation

Rates of nitrogen mineralization were assessed using an in situ incubation method (Eno 1960). Two cores of both mineral soil and forest floor (FH layer) were removed from each forest floor disturbance plot and placed in 25 micron thickness polyethylene bags (Leeson Polyfilm Manufacturing Ltd., Edmonton AB). Cores were 7cm long x 5 cm diameter, each taken directly above or below the mineral-organic interface (Figure 2.2). Cores were returned to the holes from which they were taken and litter was replaced on top. A second series of cores of the same size – two mineral and two FH – were removed from a nearby location for measurement of initial NH_4^+ and NO_3^-, and frozen until analysis. Removal of initial cores and installation of incubated cores was done between July 6-10, 1999. Buried cores were removed in the first week of October 1999 and frozen until analysis.

For analysis, cores were thawed and pairs of mineral or organic soil from the same forest floor disturbance plot were bulked and mixed by hand, removing any stones, chunks of wood or large roots. It is acknowledged that variability amongst cores in terms of the presence of stones, large roots or chunks of wood – though minimal – introduced some degree of experimental error which was not accounted for. Duplicate subsamples of approximately 10g or 20g of oven-dry mass equivalent (for organic and mineral, respectively) were extracted by placing each sample in 100mL of 2N KCl and shaking for one hour on a shaker table. Another set of duplicate subsamples was taken at the same time and oven-dried for moisture determination ($105°C$ for mineral samples and $68°C$ for organic). Extractions were filtered (Whatman 40) and analyzed for NH_4^+ and NO_3^- using a Technicon Autoanalyzer. Nitrogen mineralized during the incubation was calculated by subtracting initial NH_4^+ and NO_3^- from measured levels in the incubated cores.

Vegetation sampling

In late July 1999, percent cover of herbaceous plants was visually estimated using five systematically placed 50 cm diameter circular plots per forest floor disturbance plot (one in each corner and one in the centre). In August 1999 and 2000, species, stem length, and percent cover of *E. angustifolium, Viburnum edule, Rosa acicularis*, and *Populus* spp. were evaluated within either a single 1.5m X 1.5m quadrat centred in the plot (for burn, control, mix and scalp treatments) or four, 84.5cm diameter circular plots centred on mounds (4 X 84.5cm circular plots are the equivalent area as the 1.5m X 1.5m quadrat). Total stem length was used as a non-destructive estimate of biomass in each plot, and was calculated for each plant species by adding together the individual sstem lengths.

Light measurements

Photosynthetically active radiation (PAR) was measured during the last week of August and 1st week of September 1999 using a hand-held integrating radiometer (Sunfleck Ceptometer, model SF-80, Decagon Devices Inc., Pullman, Washington) under uniformly overcast conditions. Light readings were taken at ground level, seedling tip, and at 1.3 m in for each seedling height in every forest floor disturbance plot. There were virtually no shrubs greater than 1.3 m height thus the 1.3 m height was considered to provide a measure of light above the shrub canopy. Readings at each height consisted of two right-angle measurements centred at the seedling and then averaged. Forest floor disturbance plot-level measurements were derived for each height by averaging light measurements for all seedlings in the plot. Simultaneous open-sky PAR measurements were made in nearby clearings using a PAR sensor (LI80S, Li-Cor Inc., Lincoln, Nebraska) linked to a data logger (CR21X, Campbell Scientific Co., Ltd., Logan, Utah). Light was characterized in terms of below canopy light environment, seedling light environment and ground-level light environment, as follows:

% canopy light transmission = PAR below tree canopy (1.3m) / PAR above canopy*100

% ground-level light transmission = PAR at ground-level / PAR at 1.3m height * 100

% seedling-level light transmission = PAR at seedling-tip / PAR at 1.3m height * 100

% actual ground-level light transmission = PAR at ground level / PAR above canopy * 100

% actual seedling-level light transmission = PAR at ground level / PAR above canopy * 100

Statistical analyses

A general linear model for split-plot experimental design (Statistical Analysis System Institute Inc., Cary, NC) was used to test for significant treatment and interaction effects. The general model used in the analysis was:

$$Y_{ijk} = u + B_i + H_j + BH_{ij} + F_k + HF_{jk} + BHF_{ijk}$$

where B is the block (I = 1, 2, or 3), H is the harvest intensity (j = 1 or 2), F is the forest floor disturbance (k = 1, 2, 3, 4 or 5). Block was a random factor, while harvest intensity and forest floor disturbance were fixed factors in the model. Multiple comparisons were made using Tukey's HSD test. Significance was evaluated at p<0.10 out of a concern that the limited replication would result in a high number of Type II errors at p<0.05.

Simple correlations of single environmental or nutrient measures with single vegetation measures were performed using the PROC REG procedure in SAS (Statistical Analysis System Institute Inc., Cary, NC), and were compiled into a correlation matrix.

Results (ANOVA summary Table 2.1)

Soil Temperature

Soil temperature at 5 cm depth was significantly higher with complete canopy removal (p=<.0001; Tables 2.1-2.2) and was also affected by forest floor disturbance (p=<.0001). However, there was an interaction between canopy and forest floor disturbance (p=.0078; Figure 2.3). CC-mound treatments had higher temperatures than all other treatment combinations, while PC-mound treatments had higher temperatures than all other forest floor treatments in the PC. The scalp treatments had the second highest temperatures in the CC, however this was not the case under the PC (second lowest temperature).

Soil temperature at 20 cm depth was significantly affected by canopy removal (p<.0001; Tables 2.1-2.2), with higher temperatures measured in the CC than in PC

stands. Forest floor disturbance also had a significant effect on temperature at 20 cm (p<.0001; Figure 2.4); the highest temperatures were observed in the mound treatment, followed by the scalp treatment, while temperatures were lower in the burn and mix treatments. The lowest temperatures were noted in the control plots.

Soil moisture

Soil moisture content in the organic layer was significantly affected by forest floor disturbance (p=.0108; Figure 2.5). The mound treatments reduced soil moisture compared to all other treatments. Soil moisture content in the mineral layer was also affected by forest disturbance (p=<.0001; Figure 2.6), with lower soil moisture content noted for the mound treatments compared to all other treatments.

Nutrient Availability (Resin Bags)

Forest floor disturbance treatments had a significant impact on available NH_4^+ (p=.0023; Figure 2.7). The treatment effect was attributable to higher NH_4^+ levels in burn treatments relative to all other treatments. There was a difference in measured NO_3^- availability between forest floor treatments (p=0.0077; Figure 2.8). The burn and scalp treatments had higher NO_3^- levels than controls. Total nitrogen availability was significantly affected by forest floor treatments (p=.0113; Figure 2.9), with the burn treatment having higher N availability than control, mix and mound treatments.

Forest floor disturbance treatments had significant impacts on P availability (p=<.0001; Figure 2.10). The burn treatment had the highest P availability, control and mix treatments were intermediate, and mound and scalp treatments had the lowest P availability.

Available Ca was affected by forest floor disturbance (p=.0002; Figure 2.11); levels were high for scalp, burn and mix treatment compared to control and mound treatments. Magnesium availability was affected by harvest intensity (p=.0278; Tables 2.1-2.2) with greater Mg availability measured in the clearcut. Magnesium availability was also affected by forest floor disturbance (p=<.0001; Figure 2.12). Magnesium availability was greater in scalps than in burn, control and mound treatments, greater in mix treatments than control and mound treatments, and greater in the burn than control

and mound treatments. Potassium availability was significantly affected by forest floor disturbance (p=<.0001; Figure 2.13). Burn treatments had elevated K levels relative to control, mound and scalp treatments, and control and mix treatments had higher K availability than mound and scalp treatments.

Net N mineralization

Net N mineralization in the organic layer was significantly affected by forest floor disturbance (p=.0004; Figure 2.14). Mound treatments showed higher net N mineralization than burn and mix treatments, while net N mineralization was lower in the mix treatment than in the control.

In the mineral soil layer, forest floor disturbance had a significant effect on net N mineralization (p=.0013). However, the effect of forest floor disturbance varied with canopy treatment (p=.0354; Figure 2.15). In the CC, both burn and control treatments had higher N mineralization than the mix treatment, while in the PC, burn, control and mix did not differ.

Light transmission

Light transmission through the shrub/herb layer was different among the forest floor disturbance treatments. Shrub-herb light transmission to ground-level was significantly affected by forest floor treatment (p=.0021; Figure 2.16) with mix and mound treatments having higher shrub-herb light transmission to ground level than burn, control and scalp treatments. Shrub-herb light transmission to seedling-level was also affected by forest floor treatment (p=.0292; Figure 12.7) with mix treatments having higher light transmission than control and scalp treatments. Actual light transmission to ground-level and seedling-level was substantially lower in the PC forest floor disturbance plots than in the CC (Figures 2.18-2.19).

Vegetation

Plant density (summary in Appendix A)

E. angustifolium density was not affected by the treatments in year 1 (Figure 2.20) (data only available for first year). *V. edule* density (Figure 2.21) was significantly

affected by forest floor disturbance in both the first (p=.0028), and second year
(p=0.0414). In the first year, *V. edule* density was significantly higher in control and
burn treatments than mix and mound treatments, and higher in the scalp treatment than
the mound treatment. In the second year, *V. edule* density was only higher in the burn
treatment compared to the mix and mound treatments. *R. acicularis* density (Figure 2.22)
was not significantly affected by any treatments in the first year. In the second year, *R.
acicularis* density was higher in the CC (p=.0096; Tables 2.1-2.2) and was affected by
forest floor disturbance (p=.0247), with higher density in mounds than in all other
treatments. *Populus* spp. density was greater in clearcut stands in both the first
(p=0.0253) and the second year (p=0.0164) (Tables 2.1-2.2). *Populus* spp. density was
also affected by forest floor disturbance in the first (p=.0003) and the second year
(p=.0023) with the scalp treatment promoting greater shoot density than all other
treatments (Figure 2.23).

Percent cover (summary in Appendix B)

Percent cover of herbaceous species (Figure 2.24) was significantly affected
(p=<0.0001) by forest floor disturbance (data only available for year 1). Mix and mound
treatments had significantly lower herbaceous cover than burn, control and scalp
treatments.

E. angustifolium percent cover (Figure 2.25) was significantly affected by forest
floor disturbance in the first year (p=.0038), with the burn treatment having higher
percent cover than control, mix, and scalp treatments while mounds had higher percent *E.
angustifolium* cover than the mix treatment. In the second year, *E. angustifolium* percent
cover continued to be affected by forest floor disturbance (p=0.0076), although the mix
was no longer significantly lower than burn and mound treatments.

V. edule percent cover (Figure 2.26) was affected by forest floor disturbance in
the first (p=.0406) and the second year (p=.0092) with control plots having higher percent
cover than mix and mound treatments and, in the second year, burns were higher than the
mix treatment.

R. acicularis percent cover (Figure 2.27) was significantly affected by forest floor
disturbance in the first (p=.0112) and second year (p=.0128). However, there was a

significant interaction between canopy retention and forest floor disturbance in both the first (p=.0048) and second year (p=.0551). Control plots in the PC had higher percent cover of *R. acicularis* compared to all other forest floor treatments except for the burn in both years, whereas percent cover in control plots in the CC only differed in the second year due to increased cover in the mound treatment.

Populus spp. percent cover was significantly higher in clearcut than partial cut stands in the first (p=.0038) and the second year (p=.0368) (Tables 2.1-2.2). Forest floor disturbance also significantly affected *Populus* spp. percent cover in the first (p=0.0104) and second year (p=.0044), with scalp treatments having higher cover than burn, control and mix treatments in the first year, and greater cover than mix and mound treatments in the second year (Figure 2.28).

Total percent cover for all plants (Figure 2.29) was significantly affected by forest floor disturbance in the first (p=.0006) and the second year (p=.0933), with mix treatments having significantly lower percent cover than burn, control (first year only), mound and scalp treatments while mounds had lower percent cover than scalp treatments.

Total stem length (summary in Appendix C)

Total stem length for *E. angustifolium* (Figure 2.30) within plots was not significantly affected by the treatments in the first year but was significantly affected by forest floor disturbance in the second year (p=.0839), although no comparisons showed significance.

V. edule total stem length (Figure 2.31) was affected by forest floor disturbance in the first year (p=.0130) with control plots having higher stem length than mix and mound treatments. *V. edule* total stem length was affected by forest floor disturbance in the second year (p=.0150) with mix having lower *V. edule* stem length than burn or control treatments.

R. acicularis total stem length (Figure 2.32) was affected by forest floor disturbance in the first (p=.0025) and second year (p=.0077). However there was an interaction between canopy retention and forest floor disturbance in both the first (p=.0085) and the second year (p=.0302). In the first year, PC-control treatments had significantly higher cover of *R. acicularis* than any other forest floor treatments except

the burns, while in the CC, percent cover was not different between forest floor treatments. In the second year, mounds had the highest total stem length in the CC, while controls had the highest stem length in the PC.

Total stem length of *Populus* spp. (Figure 2.33) was significantly higher in the clearcut than partial cut treatment in the first (p=.0063) and second year (p=.0487) (Tables 2.1-2.2). Forest floor disturbance also significantly affected *Populus* spp. stem length in the first (p=0.0266) and the second year (p=.0100), with the scalp treatment having higher total stem length than the mix and mound (second year) treatments. Total stem length for all plants (Figure 2.34) was affected significantly by forest floor disturbance in the first (p=.0616) and second year (p=.0450) with the mix treatment having lower total stem length than burn and scalp treatments in the first year, and lower total stem length than the mound and scalp treatments in the second year.

Correlation of vegetation with microclimatic variables and nutrients

Vegetation measures correlated significantly with a number of variables, depending upon the vegetation type (Tables 2.3-2.5). The correlations were generally consistent for vegetation development between year 1 and year 2 (unless otherwise noted). *E. angustifolium* shoot density was correlated with moisture and Ca, while cover and stem production were correlated with moisture. *V. edule* shoot density was correlated with net NO_3^- production and moisture, cover was correlated with temperature, and stem production was correlated with net NO_3^- production, moisture and temperature. *R. acicularis* shoot density was correlated with available NO_3^-, and year 2 shoot density was correlated with temperature. *R. acicularis* cover was correlated with Mg and shoot production was correlated with both Mg and temperature. *Populus* spp. shoot density was correlated with moisture, P, Ca, Mg and K, while both cover and shoot production were correlated with moisture, Ca and Mg. Total shoot density was correlated with moisture, P, Ca, Mg and K, while total cover and total shoot production were correlated with moisture, Ca and Mg.

Discussion

Burning

Despite the limited amount of forest floor consumption by the burn treatment, nutrient availability was altered significantly by burning. An increase in nutrient availability is generally observed following fire (Wells et al. 1979), as was the case in this study where NH_4^+ and NO_3^-, P, Ca, Mg, and K availability were all elevated compared to the control. Short-term increases in available NH_4^+ (Raison 1979) and NO_3^- (Bauhus et al 1993), are typically seen following slash burning. Evidence from slash burning in harvested sites indicates that ash inputs from surface slash consumption generally contribute to increases in P, Ca, Mg, K and pH (Feller 1982, Macadam 1987). However, duff consumption in the present study (approximately 10%) was much less than most studies. Under similar conditions of light experimental burns in black spruce stands, only weak increases in available P were observed (Dyrness and Norum 1983). Light surface burns caused by wildfire in white spruce stands in Alaska resulted in increased P availability, however unlike the present study, Ca, Mg and K availability did not increase, except where there was substantial forest floor consumption (Dyrness et al. 1989). Compared to this latter study where the burn occurred in a mature unharvested stand, the burns in the present study occurred in harvested stands covered in logging slash. Branch and foliage slash contribute significant amounts of nutrients to a site (Feller 1982) and thus the presence of logging slash, rather than the amount of forest floor consumption, is most likely responsible for the observed increase in Ca, Mg, K and P availability. Results from comparable low intensity prescribed burns in other white spruce dominated stands are not available. Macadam (1987) evaluated nutrient responses in forest floors following low intensity prescribed burns (approximately 25% forest floor reduction) in lodgepole pine/spruce stands in British Columbia and saw increased Ca, Mg, and P availability compared to unburned controls.

The elevated nutrient availability in this study following burning could also be ascribed to changes in microbial activity and mineralization rates. Higher temperatures in the burn treatment could have increased microbial activity (Covington and Sackett 1986). The pulse in nutrient availability following forest floor disturbance could also have stimulated microbial activity and increased further nutrient release (Covington and

Sackett 1986, Krause and Ramlal 1987). Nonetheless, despite higher temperatures and higher nutrient availability, the incubations did not indicate an increase in net N mineralization relative to the unburned control. It may be that the temperature increase, though statistically significant, was so slight (<1°C) that it did not affect mineralization.

Despite no differences in mineralization activity, soil heating during the fire, as well as the post-fire environment may have affected the composition of the microbial community and its nutrient transformations. Indeed, there was a notable increase in NO_3^- availability over the unburned control. Soil heating attributable to fire is known to have a more severe impact on fungi and may enhance bacterial transformations (Pietikäinen and Fritze 1995). Previous studies have noted increases in the abundance of nitrifying bacteria and levels of nitrification following slash burning (Jurgenson et al . 1981), a process that is associated with increased base cation availability (Bauhus et al. 1993, Ste. Marie and Paré 1999). Higher NH_4^+ availability, such as seen in the burns, would have been necessary for higher nitrification, however a correlation between NO_3^- production and NH_4^+ availability indicated a much stronger relationship when the base cations Ca and Mg were included (data not shown). The observed increase in base cation availability following the burn may thus have played a role in stimulating nitrifiers and higher levels of NO_3^- production.

Mixing

The mixing treatment increased Ca and Mg availability relative to the control, while N, P and K availability did not differ. MSP treatments that mix mineral soil should result in increased base cation availability, because of the high exchange capacity and base cation status of the mineral soil (Schmidt et al. 1996). Krause and Ramlal (1987) also observed increased Ca and Mg availability in clearcuts following mixing of the forest floor and upper mineral soil. However, in contrast to my study, they also found decreased N and P availability.

It has been suggested that soil mixing, by improving aeration, may promote decomposition and improve nutrition (Prescott et al. 2000a, Mallik and Hu 1997). However, my results suggest that N availability was diminished by the mixing of mineral soil with the forest floor. Mixing did not result in higher N availability (either NO_3^- or

NH$_4^+$) and net N mineralization in the forest floor was the lowest in the mixing treatment. Keenan et al. (1994) also found that decomposition and mineralization were either unaffected or diminished by mixing. It is likely that reductions in mineralization resulting from mixing are driven by higher N immobilization, as incorporation of labile C substrates (litter and logging residue) increases microbial immobilization (Vitousek and Matson 1985, Thibodeau et al. 2000). This study did not measure decomposition rates and thus it is not clear whether decomposition rates increased or decreased, but microbial biomass could have taken up much of the available N. Mallik and Hu (1997) measured higher respiration rates in mix treatments, suggesting microbial activity is enhanced by mixing. Consequently, decomposition could be higher in the mix treatment while at the same time mineralization is lower for the period after mixing. Given this scenario, mineralization would eventually release immobilized N at some later stage.

Mounding

Availability of Ca, Mg, K and P was consistently lower in the mounds compared to other treatments, while N availability was not significantly different. However, nutrient availability as measured by resin bags in the mounds probably do not give a fair integration of nutrient availability relative to the other treatments. In all other treatments, resin bags were placed in the mineral horizon below the residual organic horizon, and thus would absorb ions through diffusion and downward movement of soil water from the organic horizon above. However, in the mounds the resin bags were situated in the mineral cap above the buried organic layer and thus nutrients released from the organic horizon would not have been captured by the resin bag. Previous studies have shown higher nutrient availability within the buried organic layer of the mound (Lundmark in Örlander 1990), an effect attributable to higher mineralization rates (Örlander 1990). Soil mixing, cycles of wetting and drying and higher temperatures are thought to drive increased microbial activity in mounds (Örlander 1990, Johannson 1994).

Net N mineralization rates in the organic layer were clearly higher in the mound treatment relative to the burn and mix treatments, and although not statistically significant, appeared higher than in the control. Temperatures were much higher in the

mounds than the other treatments (figures 1-2), and thus higher biological activity would be expected (Lundmark-Thelin and Johansson 1997). Moisture is also an important factor affecting microbial activity (Bunnell et al. 1976) and moisture availability was notably lower in both the mineral cap and buried organic layer of the mound. Given the high net N mineralization in the organic layer of the mound, it appears that increased temperatures were driving higher rates of net N mineralization. The mineral horizon of the mound experienced even higher temperatures than the organic layer, but the low moisture availability likely constrained biological activity, thus reducing net N mineralization. Indeed, when initial moisture level of the incubated mineral core was accounted for by using it as a covariate, mineralization rates were much higher in the mineral cap of the mound compared to mineral cores in the other treatments, further suggesting moisture constrained mineralization rates in the mineral layer of the mound.

A recent study of mound nutrient dynamics by Smolander et al. (2000) found results which contrast with this study. Within the buried organic layer they found a trend towards equivalent or decreased rates of net N mineralization relative to mineralization in the unmounded forest floor. An explanation they offered was that incorporation of logging residues in the mounds stimulated microbial demand for N thereby limiting N mineralization. There was also some incorporation of logging residues in mounds in the present study, but it is not clear if it was to the same extent. They did not measure temperature or moisture, however given that their mounds were smaller than in my study, the temperature increases were likely to be less important. Furthermore they sampled the buried inverted organic layer together with the underlying (uninverted) forest floor layer, whereas my incubations were done with organic matter immediately below the mineral cap. Higher temperatures were evident directly below the mineral cap, however the temperature differences disappeared deeper into the mound. This is noteworthy, as it suggests that enhanced microbial activity, driven by higher temperature, may not occur deeper in the mound. This may also be a contributing factor in the apparent trend towards decreased mineralization noted by Smolander et al. (2000). Together, these contrasting results for nutrient dynamics highlight the spatial complexity of mounds and the need to consider a host of properties including the size of the mounds, their thermal

properties, moisture dynamics and the amount of residue incorporation when evaluating nutrient responses and potential effects on planted tree seedlings.

Scalping

Nitrate, Ca, and Mg availability were all increased by the scalping treatment compared to the untreated control, and there was a trend towards higher total N availability as well (p=.1375). In contrast, MSP treatments involving the removal of the forest floor have been shown to decrease available NH_4^+ and NO_3^- (Krause and Ramlal 1987, Munson et al. 1993) and decrease available Ca, Mg, K and P (Krause and Ramlal 1987). This decrease in availability may result from the loss of the nutrient reservoir in the forest floor (Munson et al. 1993). As in my study, Munson and Timmer (1995) found that forest floor removal had a positive effect on N availability, an effect possibly attributable to the absence of the forest floor (which would tend to immobilize N) or to increased mineralization stimulated by higher temperatures.

There appeared to be no effect of scalping on net N mineralization. This is somewhat surprising given that the incubated mineral cores in the scalps were almost at the surface and experienced much higher temperatures than in the burn, control and mix treatments (where the mineral soil was insulated by the surface organic matter). Given that mineralization did not increase in the upper mineral soil, it seems likely that the increased N availability observed on the resins must have been driven by nutrient release in the thin (2cm thick) H layer that was retained in the scalps (and that was not contained in the net N mineralization core). Mineralization in the H layer has been shown to increase with exposure to higher temperatures (Verburg et al. 1999). The H layer in the scalping treatment averaged about 5°C higher than the equivalent H horizon temperature in other treatments (except the mound). Thus, it is likely that higher temperatures increased mineralization in the exposed H layer resulting in higher N availability. At the same time, the absence of more decomposable L and F layers would have reduced C substrates and thus diminished N immobilization (Vitousek and Matson 1985, Munson and Timmer 1995). Consequently, higher N availability was apparent.

Nitrate availability was also higher in the scalps, suggesting higher levels of nitrification. Stimulation of NO_3^- production was also observed by Munson et al. (1993)

in incubated cores of mineral soil from scalped areas. However, increased NO_3^- production was not reflected in increased NO_3^- availability in their resin bags. The opposite trend was evident in my study with high NO_3^- levels on the resins, but no difference in NO_3^- production in the incubated cores. This again suggests that changes in N availability were being driven by dynamics in the thin humus layer retained in the scalp, rather than changes in activity in the mineral soil.

Vegetation

Vegetation was dominated primarily by *E. angustifolium*, *V. edule*, *R. acicularis* and *Populus* spp, while density and cover of other species of shrubs and herbs was minimal. Establishment by these dominant species was primarily vegetative, as is typically seen where forest floor consumption is limited (Dyrness et al. 1986). Burning of the forest floor is known to have significant impacts on vegetation response (Rowe 1983, Dyrness et al. 1986). In the present study, the burning was concentrated at the surface and did not penetrate deeply. In the case of *E. angustifolium*, the burning treatment stimulated higher *E. angustifolium* cover. Given that there was no detectable increase in *E. angustifolium* density following burning, it appears that individual plants produced more cover, an effect likely attributable to higher nutrient availability. *E. angustifolium*'s ability to take up nutrients is very high (Dyrness and Norum 1983, van Andel and Vera 1977) and *E. angustifolium* has been shown to increase its cover with fertilization (Reinikeinan in Myerscough 1980). It may also be that burning delayed responses from other less vigorous colonizers, thus *E. angustifolium* plants were able to establish first and dominate the burns. Burning did not appear to diminish or stimulate other vegetation. Light burns in the boreal mixedwood of central Saskatchewan stimulated increased aspen density (Peltzer et al. 2000), but there was no evidence that my burns stimulated aspen response. Burns in the present study increased temperatures only slightly, and temperature is thought to play an important role in aspen suckering (Maini and Horton 1966, Lavertu et al. 1994). *V. edule* and *R. acicularis* are both capable of resprouting from stems after fire (Rowe 1983, Parminter 1983) and thus burning did not appear to significantly affect their cover in this situation.

The mixing treatment disturbed both the forest floor and upper 2-3 cm of the mineral soil, fragmenting the materials in that zone. This is a zone where many of the regenerative structures of these plants are typically found, so it is unlikely that any plants in the zone of mixing would have survived. As a consequence, vegetation was most reduced in this treatment. Keenan et al. (1994) also found that mixing was highly effective in reducing vegetation competition in coastal British Columbia. Nonetheless, some plants did sprout, probably from roots and rhizomes situated below the mixing depth. Both *R. acicularis* and *E. angustifolium* are known to be rooted in the mineral soil (Moss 1936, Myerscough 1980, Calmes and Zasada 1982), and this deeper rooting depth may have allowed them improved establishment relative to *V. edule* or aspen. Sprouting could possibly occur from fragmented root and rhizome segments in the mixing zone. However, in many plant species, belowground storage reserves can be an important factor in the successful regeneration of root or rhizome segments (Hogg and Lieffers 1991b, Broderick 1980) so smaller segments would have difficulty sprouting. Planted root segments of *E. angustifolium*, for example, may produce shoots only when they are at least 8 cm or longer (Broderick 1980).

Mineral-capped mounds are used in the northern boreal forest for control of competing vegetation (Landhäusser and Lieffers 1999).   Nonetheless, there was considerable establishment of *E. angustifolium* and *R. acicularis* in some of the mounds in this study. This response is reasonable given that mounding placed the mineral soil on top of the mound, increasing temperatures in this region. Roots and rhizomes of species rooting in the mineral soil would be favoured by this treatment, because inverting the soil would both place perennating structures closer to the soil surface and expose them to higher temperatures. For *R. acicularis*, high sprouting became especially evident in the second year. In addition mounding resulted in some degree of cutting and breakage of rhizomes during the creation of the mound. This may also have favoured *R. acicularis* and *E. angustifolium*, as both are stimulated by cutting (Hardy BBT Limited 1989, Coates and Hauessler 1986).   The high nutrient availability may also have contributed to higher cover of those plants establishing on the mounds.

The scalping treatment removed most, but not all of the forest floor, likely removing some root and rhizomes but also exposing or placing many roots and rhizomes

closer to the surface. This treatment also resulted in temperature increases, although not to the same extent as the mounds. This treatment clearly favoured suckering by aspen and poplar roots. Scarification of the forest floor has been shown to increase suckering (Lavertu et al. 1994, Maini and Horton 1966). It is not clear whether this is attributable to root wounding or temperature increases (Lavertu et al. 1994). Heavier drag scarification resulted in higher suckering (Weingartner 1980), suggesting disturbance must be to a sufficient depth. However, relative high intensity MSP treatments such as drum-chopping have been shown to reduce aspen regeneration (Peltzer et al. 2000), and the more severe mounding or mixing treatments in the present study reduced aspen cover and density. It thus appears that some level of forest floor disturbance is needed, but if too severe will reduce aspen establishment.

The scalping treatment, which unlike the mixing and mounding treatments did not disrupt the mineral soil layer, was the most favourable of the different treatments imposed for promoting aspen suckering. In contrast, scalping was observed to significantly reduce aspen sucker density relative to burning or no forest floor disturbance in the boreal mixedwood of Saskatchewan (Peltzer et al. 2000). Scalping depth will likely determine plant regeneration, as deep scalps which remove roots and rhizomes of understory plants have been shown to reduce understory plant development for 5 years (Lees 1970). Scalping did not appear to increase *E. angustifolium* or *R. acicularis*, suggesting that exposure alone was not sufficient for these plants. Temperatures were not as high here as in the mounds which may have limited the response of *R. acicularis* and *E. angustifolium*. As well, the scalping treatment probably did not result in the same degree of breakage of roots and rhizomes which may have hindered sprouting compared to the mounds.

Correlation of vegetation with microclimatic variables and nutrients

Correlations between nutrients and vegetation were strongest for Ca and Mg (the two of which were highly correlated themselves), notably for *Populus* spp., but also for *E. angustifolium*. The presence of *Populus tremuloides* has been observed to have a positive effect on Ca availability (Brais et al. 1995). *Populus tremuloides* has a relatively high demand for Ca (Alban 1982) so high availability may have contributed to its more

vigorous establishment. Given the importance of fire and plant adaptations to it, it would be reasonable to suggest that sprouting could be stimulated by increased nutrient availability, and specifically by base cations or the accompanying pH change. The relationship between Ca/Mg and vegetation could thus be a reflection of the importance of Ca, Mg, or pH, or their correlation with some other driving factor.

Vegetation cover and shoot growth were also correlated with soil moisture. It was a fairly dry summer in 1999, so moisture may have been an important constraint on growth. Correlations between vegetation and nitrogen were weak to non-existent, as has been noted in other studies (e.g. Messier and Kimmins 1992). This is surprising given that N is generally limiting in boreal forests. Moreover, Thevathasan et al (2000) recently found that increased nitrogen availability benefited competing vegetation. The fact that only a few weak correlations were found between N and vegetation suggests that moisture limitation may have been overriding any effects that increased availability in nitrogen may have had.

Canopy effects

The impact of disturbance on nutrient dynamics was primarily driven by forest floor disturbance, with only limited effects attributable to harvest intensity (Table 2.9). There was higher Mg availability in clearcuts and a trend towards higher Ca in clearcuts as well (p=.155). However, a much stronger influence of canopy on both nutrient availability and rates of mineralization was expected. Different temperature and moisture conditions resulting from variable levels of tree removal between clearcuts and partial cuts should result in different levels of microbial activity and rates of mineralization (Bunnell et al. 1976, Binkley 1984, Prescott 1997). Temperature and moisture availability will not be as high in partial cuts and thus microbial activity should not be stimulated to the same degree as in a clearcut. Moreover, partial cuts should have lower forest floor nutrient availability due to nutrient uptake by the residual standing trees. Prescott (1997) found that rates of N mineralization were altered less by silvicultural systems that maintained different levels of standing trees than were clearcut stands. In contrast, Kim et al. (1996) found that there was little effect of differing levels of canopy removal on decomposition and nutrient release in red oak and red pine stands. It may be

that the effect of canopy removal on decomposition or nutrient dynamics is buffered by compensation among the different forest floor horizons (Yin et al. 1989). For example, moisture levels in a partial cut, though lower than a clearcut, may be more ideal for microbial activity and thus compensate for any effect of higher temperatures on microbial activity in the clearcut. This may explain the lack of a clear trend of increasing canopy removal on N mineralization, and the resulting inability to predict nutrient responses based on basal area removal (Prescott 1997).

It is also possible that nutrient uptake in the forest floor disturbance treatments by residual trees in the partial cut may not have been as important as expected. First, the removal of trees in the partial cut would have left many root inactive. Second, the disturbance treatments all disrupted the forest floor to some degree, whether through mixing, scalping, mounding or heating during fire. As a result, many of the active roots in these areas of the forest floor disturbance plots would have been destroyed. It may be that uptake in the disturbance plots was thereby substantially limited, resulting in nutrient availability not dissimilar to the clearcuts, where there was no active tree uptake of nutrients.

By removing all trees, clearcutting decreases C pools in the soil through diminished exudation and rhizosphere activity (Hendrickson and Robinson 1984). Therefore microbial activity should be more limited in the CC, and immobilization should not be as high. However, if the forest floor disturbance disrupts rooting activity substantially, the effects of retained trees in terms of rhizosphere activity and exudation will be severely diminished. Given this, there is less likely to be a difference between the CC and PC in terms of their ability to immobilize nutrients. Still, there are different abiotic factors potentially affecting microbial activity, so while temperatures may be more optimal in a clearcut, the moisture conditions may not be and thus compensation between temperature and moisture will diminish any differences in microbial activity between CC and PC.

Canopy retention did not have a clear impact on vegetation, despite the fact that vegetation cover is frequently related to canopy cover and light availability (Lieffers and Stadt 1994). There was a clear difference for aspen suckering between harvesting levels, with greater aspen development in the CC. While aspen regeneration is stimulated by

partial cutting, the greatest suckering response is associated with clearcutting (Shier and Smith 1979). Thus for this study the response of aspen fit with the well established response patterns observed in other studies. Canopy retention did not appear to reduce cover, density and height of the other plant species, relative to the CC. This may be a function of the degree of mechanical damage to aboveground parts in different harvesting types (Moola et al. 1998, Thomas et al. 1999). Disturbance associated with the CC harvest destroyed aboveground plant parts, whereas limited harvest damage in PC retention strips allowed some established shrubs to persist. Plant sampling did not discriminate between sprouts and established plants, but it is likely that plants that escaped damage in the PC contributed to density, cover and height measurements that were not significantly different from the CC (where plants had to resprout from stored reserves). For this reason there may be a time lag in the recovery of vegetation following canopy removal (Thomas et al. 1999). It is reasonable to expect that over the longer term lower light levels in the partial cut, which will likely continue to decrease with canopy development, will limit survival and growth of understory plants.

There was also a fair degree of microsite variability within the study area, and this may have constrained the ability to see stronger effects of the canopy treatments. Spatial variability in preharvest vegetation, differences in forest floor depth, variation in vertical distribution of roots and rhizomes, slash distribution and forest floor nutrient status all likely contributed to the high degree of variability in the data. Indeed, it has been observed that differences in N mineralization can vary substantially between sites in spite of no evident physical/chemical differences between soils, an effect attributed to variation in understory vegetation (Prescott et al. 2000b).

Silvicultural studies are also constrained by the operational scale upon which they are typically carried out. The expense involved in applying treatments limits the ability to replicate extensively and this may have limited the ability of this study to detect canopy effects. Furthermore, there is variability associated with the installation of mechanical site preparation treatments themselves. Rarely are two prepared microsites the same, reflecting the microtopography over which site preparation equipment operates. Variability in the forest floor coupled with variability in the installation of treatments creates a significant amount of noise, making responses less clear. Nonetheless, given

the strong responses associated with forest floor disturbance it is clear that different types of disturbance at the forest floor level can have significantly different impacts. In terms of the effect of canopy, the results should be interpreted with caution, as it is not entirely clear why the effect of partial canopy retention on nutrient and vegetation dynamics was not more apparent. It may be that the effect was weaker than expected, that canopy does not control nutrient and vegetation responses in the short term, or that the effect was difficult to detect given the level of replication.

Conclusions

Disturbance at the forest floor level, either by mechanical site preparation or by low-intensity burning, significantly altered nutrient availability and rates of N mineralization. Burning and scalping treatments generally increased nutrient availability in the first season of disturbance and the mounding treatment increased N mineralization within the organic layer of the mound. Mixing, in contrast, decreased rates of N mineralization in the surface horizon. Differences in nutrient availability or cycling of N may affect planted tree seedling nutrition and growth in the longer term. High rates of mineralization or greater nutrient availability caused by the different disturbances may be of more benefit to competing vegetation in the short term, which would be to the detriment of seedling growth. Moreover, higher nutrient availability and rates of mineralization could lead to nutrient leaching and thus a loss in nutrient capital. Nutrient loss may be of greatest concern in the mounding treatment where high temperatures favour high rates of mineralization and vegetation development and uptake are limited. The burning treatment may also lead to nutrient losses due to increased nutrient availability, however the limited forest floor consumption from a low intensity burn should not reduce the forest floor nutrient capital substantially.

Forest floor disturbance also had a notable effect on vegetation. An increase in *E. angustifolium* cover during the first season following fire was seen in the burning treatment. Mounding favoured increased sprouting of *R. acicularis* by the second growing season following site preparation. Scalping promoted vigorous root suckering by *Populus* spp.. These trends in early vegetation development are important for several reasons. First, it is clear that different disturbances favour different types of vegetation,

which will in turn affect the success of planted seedlings. The high *Populus* spp. cover promoted by scalping would not be suitable for tree seedling success. Interestingly, a light scalp may be a useful site preparation for regenerating aspen. Second, the level of vegetation control differed between the treatments. Clearly, the mixing treatment offering the highest degree of vegetation control by limiting cover and thereby promoting higher light transmission. Mounding provided a reasonable level of vegetation control in most cases, although some mounds were densely colonized. Third, the fact that a certain type of disturbance can increase the dominance of a certain species may be of use for controlling other species that are more aggressive competitors. If a treatment such as a low-intensity burn can be used to increase *E. angustifolium* cover, and thereby limit the establishment of another aggressive competitor (e.g. *Calamagrostis canadensis*), it may be a useful management tool for vegetation control.

The effect of partial canopy retention on vegetation development and nutrient availability was not entirely clear at this early stage. Clearcutting tended to lead to higher Mg and Ca availability relative to the partial cut, which likely increases soil pH and the establishment of competing vegetation. The partial cut also had an effect on aspen development, limiting its density and cover relative to the clearcut. Consequently, the retention of a partial canopy was beneficial in reducing competition from aspen. The lower light conditions in the partial cut should limit the development of vegetation compared to the clearcut and thus there should be a benefit of canopy retention to planted tree seedlings in the longer term.

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Table 2.1. ANOVA summary of all variables as affected by canopy disturbance (1 degree of freedom), forest floor disturbance (4 degrees of freedom) or their interactions (4 degrees of freedom).

Variables		Canopy disturbance		Forest floor disturbance		Canopy * Forest floor disturbance	
		F	P	F	P	F	P
Soil temperature	5cm	137.51	<0.0001	78.13	<0.0001	4.86	0.0078
	20cm	128.92	<0.0001	147.37	<0.0001	1.15	0.3633
Soil moisture	organic	0.76	0.4756	5.82	0.0108	0.94	0.4511
	mineral	1.73	0.3188	25.18	<0.0001	1.83	0.172
Nutrient availability	NH_4^+	0.1	0.7728	6.73	0.0023	1.25	0.3306
	NO_3^-	1.19	0.3896	5.1	0.0077	0.47	0.7456
	$N(NH_4^+ + NO_3^-)$	2.71	0.1169	3.2	0.0379	0.09	0.9831
	P	0.43	0.5813	56.6	<0.0001	1.17	0.3617
	Ca	3.06	0.155	11.2	0.0002	0.73	0.5817
	Mg	11.41	0.0278	18.22	<0.0001	0.58	0.6807
	K	1.34	0.3109	58.3	<0.0001	0.69	0.6126
Net N mineralization	organic	0.07	0.7942	11.58	0.0004	1.75	0.2019
	mineral	2.71	0.1753	7.5	0.0013	3.36	0.0354
Light transmission	seedling-level	0.31	0.5859	3.45	0.0292	1.81	0.1703
	ground level	0.05	0.8414	6.82	0.0021	1.61	0.2213
Vegetation YEAR 1							
Density	*E.angustifolium*	0.61	0.4772	1.69	0.2017	0.41	0.8022
	V.edule	0.55	0.5351	6.41	0.0028	1.27	0.3243
	R.acicularis	0.02	0.8923	0.42	0.7954	1.55	0.2313
	Populus spp.	12.12	0.0253	9.8	0.0003	1.6	0.2231
Cover	Herbs	0.39	0.5953	37.38	<0.0001	2.17	0.1196
	E.angustifolium	0.44	0.5437	5.99	0.0038	1.44	0.2671
	V.edule	0	0.9768	3.22	0.0406	0.24	0.9128
	R.acicularis	4.1	0.1802	4.64	0.0112	5.7	0.0048
	Populus spp.	10.72	0.0038	4.39	0.0104	0.74	0.5734
	Total	1.16	0.3949	8.8	0.0006	0.5	0.7384
Total stem length	*E.angustifolium*	1.82	0.2491	2.31	0.1019	1.34	0.2968
	V.edule	0.15	0.7361	4.46	0.013	0.19	0.9406
	R.acicularis	7.48	0.1118	6.55	0.0025	4.97	0.0085
	Populus spp.	9.33	0.0063	3.46	0.0266	0.35	0.8428
	Total	2.24	0.2734	2.8	0.0616	1.22	0.3397
Vegetation YEAR 2							
Density	*E.angustifolium*	1.89	0.2408	1.75	0.1881	0.71	0.5968
	V.edule	0.28	0.6472	3.2	0.0414	0.5	0.7355
	R.acicularis	8.4	0.0096	3.62	0.0247	2.13	0.1189
	Populus spp.	15.82	0.0164	6.69	0.0023	0.4	0.8043
Cover	*E.angustifolium*	1.36	0.3084	5.11	0.0076	1.09	0.3926
	V.edule	1.28	0.3746	4.87	0.0092	0.29	0.8723
	R.acicularis	3.76	0.1922	4.48	0.0128	2.91	0.0551
	Populus spp.	9.51	0.0368	5.81	0.0044	0.48	0.7527
	Total	0.52	0.5473	2.4	0.0933	1.53	0.2411
Total stem length	*E.angustifolium*	1.37	0.3064	2.5	0.0839	1.36	2.913
	V.edule	0.28	0.6487	4.3	0.015	0.16	0.9547
	R.acicularis	1.49	0.238	4.87	0.0077	3.42	0.0302
	Populus spp.	7.86	0.0487	4.77	0.01	0.35	0.8419
	Total	1.88	0.2418	3.11	0.045	1.91	0.1584

Table 2.2. Summary of significant effects of harvest type (CC = clearcut and PC = partial cut) on environmental variables, nutrients and vegetation. Means for each harvest type are shown with standard errors in parentheses, and P values.

| Variable | Harvest Type | | P value |
	CC	PC	
Soil Temperature 5cm (°C)	19.76 (1.8)	16.71 (1.26)	<0.0001
Soil Temperature 20cm (°C)	12.89 (1.32)	11.10 (1.19)	<0.0001
Magnesium (*ug*/resin bag)	151.52 (45.38)	86.23 (21.07)	0.0278
R. acicularis (year 2) density / plot	16.83 (4.73)	12.12 (2.88)	0.0096
Populus spp. (year 1) density / plot	20.97 (13.41)	13.68 (13.8)	0.0253
Populus spp. (year 2) density / plot	16.83 (4.73)	12.12 (2.88)	0.0164
Populus spp. (year 1) cover (%)	6.12 (3.75)	2.64 (1.77)	0.0038
Populus spp. (year 2) cover (%)	9.10 (5.45)	3.19 (2.01)	0.0368
Populus spp. (year 1) stem length (cm / plot)	474.28 (296.92)	175.38 (123.59)	0.0063
Populus spp. (year 2) stem length (cm / plot)	785.4 (523.77)	232.65 (145.28)	0.0478

Table 2.3. Correlation summary for shoot density of plant species as related to soil moisture, soil temperature, net N mineralization and nutrient availability. Values presented are r², and significant relationships are indicated. (* = significant at P<0.05, ** = significant at P<0.01)

	Net N Mineralization					Available Nutrients (resin)						
YEAR 1	Net NO₃	Net NH₄	Net N	Moisture	Temperature	P	Ca	Mg	K	NO₃	NH₄	N
E.angustifolium	0.0965	0.0311	0.0022	0.3119**	0.0073	0.0121	0.1651*	0.1047	0.0048	0.0007	0.0399	0.0118
V. edule	0.2855**	0.0071	0.0928	0.2691**	0.0694	0.0031	0.0869	0.0487	0.0188	0.0237	0.0034	0.0187
R. acicularis	0.0527	0.0569	0.0201	0.0423	0.0001	0.0283	0.0119	0.033	0.0014	0.1317*	0.0009	0.0752
Populus spp.	0.0398	0.0218	0.0524	0.1453*	0.0076	0.1497*	0.3891**	0.3254**	0.2004*	0.02	0.0301	0.0006
Total	0.1182	0.0048	0.0445	0.3224**	0.0051	0.1566*	0.47**	0.3605**	0.1631*	0.0294	0.0393	0.0012
YEAR 2												
E.angustifolium	0.0943	0.007	0.0019	0.3182**	0.0702	0.053	0.1566*	0.1275	0.0129	0	0.0357	0.0074
V. edule	0.2037**	0.0002	0.0399	0.2587**	0.0523	0.0013	0.0558	0.0297	0.0291	0.0107	0.0002	0.0066
R. acicularis	0.0071	0.0663	0.0487	0.0624	0.1933*	0.0993	0.0018	0.0062	0.0184	0.0202	0.0143	0.0023
Populus spp.	0.0502	0.0174	0.05	0.2793**	0.016	0.0901	0.6749**	0.5639**	0.0913	0.0084	0.0244	0
Total	0.1262	0.0039	0.0073	0.4588**	0.0851	0.1049	0.3275**	0.2591**	0.0357	0.0037	0.0441	0.0026

Table 2.4. Correlation summary for cover of plant species as related to soil moisture, soil temperature, net N mineralization and nutrient availability. Values presented are r^2, and significant relationships are indicated. (* = significant at P<0.05, ** = significant at P<0.01).

	Net N Mineralization					Available Nutrients (resin)						
	Net NO$_3$	Net NH$_4$	Net N	Moisture	Temperature	P	Ca	Mg	K	NO$_3$	NH$_4$	N
YEAR 1												
E.angustifolium	0.0632	0.0002	0.0079	0.353**	0.009	0.0047	0.1122	0.0626	0	0.0016	0.0147	0.0069
V. edule	0.1159	0.0081	0.0027	0.076	0.2329**	0	0.0002	0.0185	0.0054	0.052	0.0017	0.0332
R. acicularis	0.0111	0.0376	0.0222	0.0188	0.0535	0.0006	0.0662	0.13	0.0003	0.0446	0	0.0226
Populus spp.	0.0421	0.0123	0.0381	0.2625**	0.0323	0.11	0.4766**	0.3872**	0.1118	0.0143	0.0134	0.0011
Total	0.1152	0.0006	0.0272	0.531**	0.0013	0.0849	0.3995**	0.2513**	0.0696	0.026	0.0193	0.0028
YEAR 2												
E.angustifolium	0.0154	0.0137	0.0042	0.1534*	0.0885	0.0222	0.0318	0.0242	0.01	0.0148	0.0342	0.0291
V. edule	0.0627	0	0.0098	0.0791	0.1681*	0.0075	0.0076	0.0287	0.0223	0.03	0.0083	0.0273
R. acicularis	0.0657	0.0738	0.0268	0.0517	0.1296	0.0036	0.0569	0.1523*	0.0004	0.0927	0.0001	0.0459
Populus spp.	0.0537	0.0099	0.0378	0.2707**	0.0124	0.0719	0.5786**	0.4915**	0.06	0.0028	0.0198	0.0006
Total	0.117	0.0245	0.0002	0.4731**	0.0109	0.0722	0.1704*	0.0869	0.0385	0.0052	0.045	0.0019

Table 2.5. Correlation summary for total stem length of plant species as related to soil moisture, soil temperature, net N mineralization and nutrient availability. Values presented are r², and significant relationships are indicated. (* = significant at P<0.05, ** = significant at P<0.01).

|	Net N Mineralization					Available Nutrients (resin)						
YEAR 1	Net NO₃	Net NH₄	Net N	Moisture	Temperature	P	Ca	Mg	K	NO₃	NH₄	N
E.angustifolium	0.0603	0.0018	0.0205	0.4006**	0.0174	0.006	0.0936	0.0463	0.0006	0.0001	0.0054	0.0006
V. edule	0.1663*	0.0001	0.0311	0.155*	0.1782*	0.0004	0.0032	0.0022	0.0116	0.0228	0.0026	0.0172
R. acicularis	0.0134	0.0272	0.0134	0.0263	0.1635*	0.0069	0.0718	0.149*	0.0007	0.0406	0.0031	0.0288
Populus spp.	0.04	0.0241	0.0561	0.2305**	0.036	0.0939	0.4573**	0.383**	0.0998	0.0067	0.0083	0.0003
Total	0.1132	0.0066	0.0484	0.612**	0.0098	0.039	0.2788**	0.1618*	0.0152	0.0086	0.008	.0007
YEAR 2												
E.angustifolium	0.0439	0.0068	0	0.3255**	0.0959	0.0574	0.0985	0.0635	0.0218	0.0005	0.0369	0.0105
V. edule	0.1758*	0	0.028	0.2015*	0.1634*	0.0001	0.0106	0	0.0167	0.0283	0.0043	0.0226
R. acicularis	0.03	0.0308	0.0105	0.1267	0.0052	0.0241	0.0362	0.0938	0.0008	0.0615	0.0001	0.0329
Populus spp.	0.0386	0.014	0.0395	0.3184**	0.009	0.065	0.6872**	0.545**	0.0628	0.0045	0.0246	0.0005
Total	0.0849	0.0007	0.009	0.5717**	0.0671	0.1002	0.3705**	0.2496**	0.0506	0.0032	0.0445	0.0029
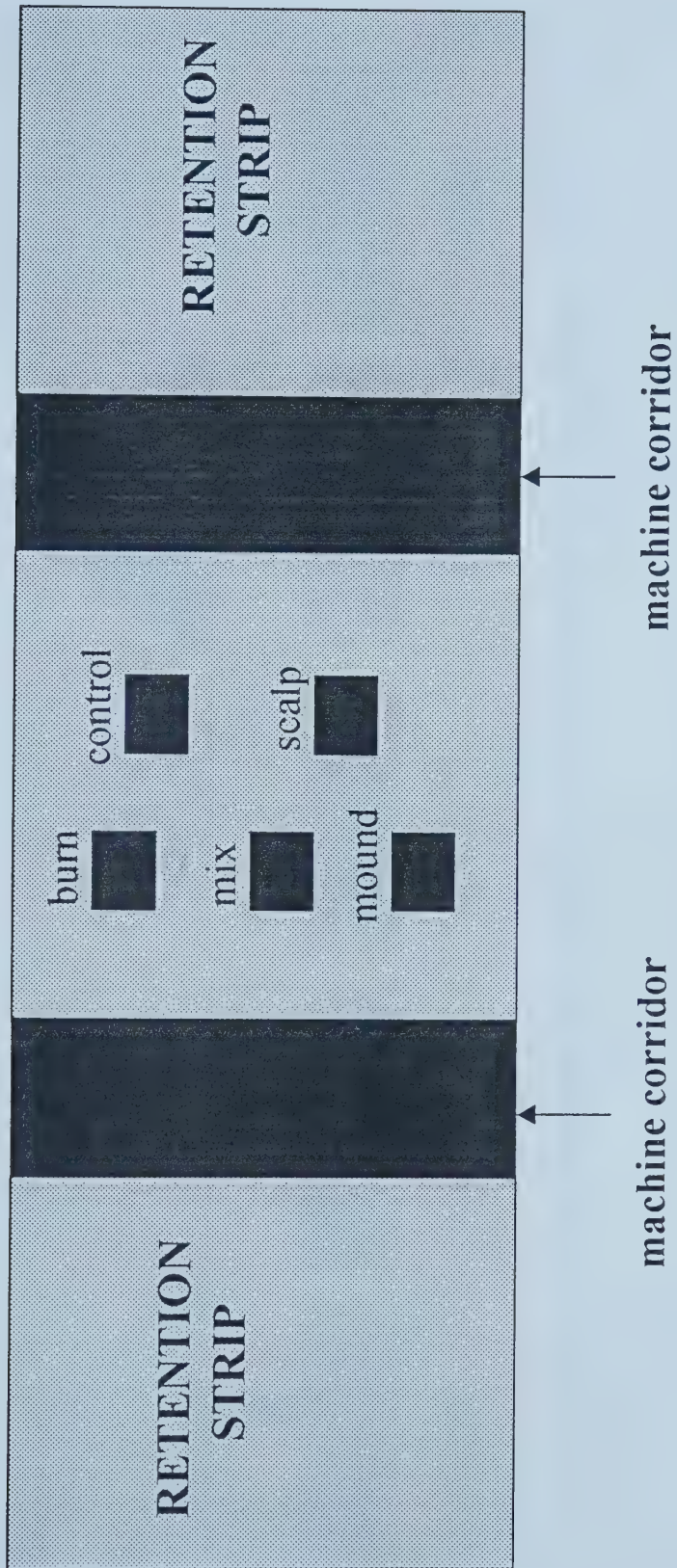
Figure 2.1. Harvesting layout in partial cut and the placement positions of the different forest floor disturbance treatments within the retention strip.
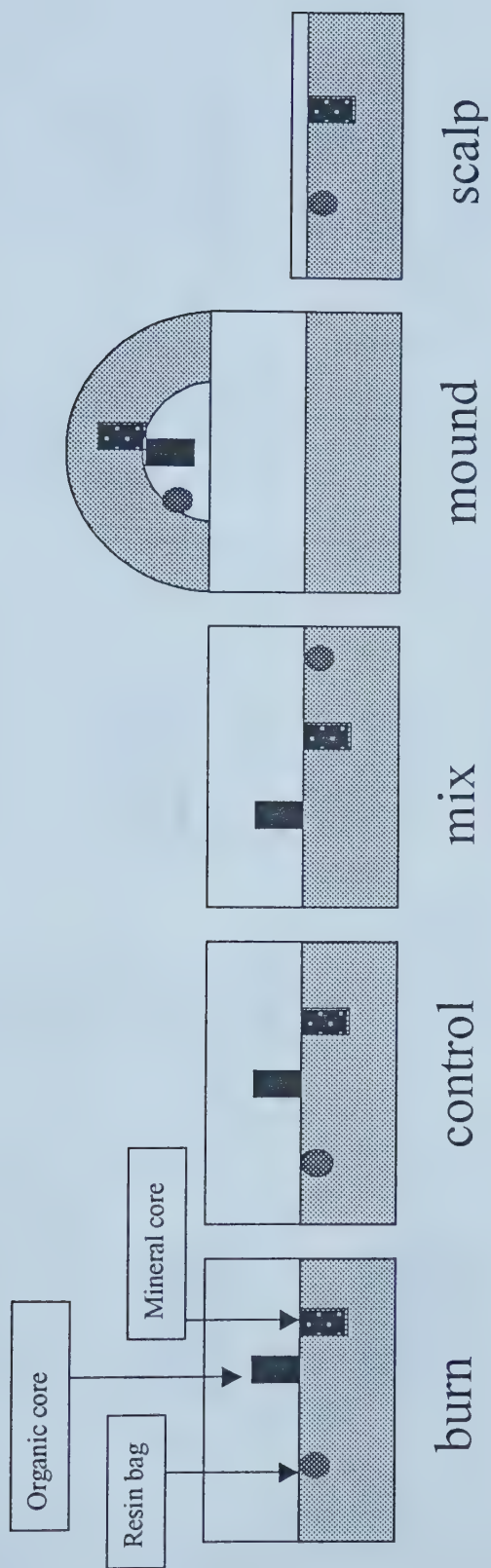
Figure 2.2. Soil horizons profiles displaying placement positions of incubated cores (net N mineralization) and resin bags (nutrient availability) in each forest floor disturbance treatment.
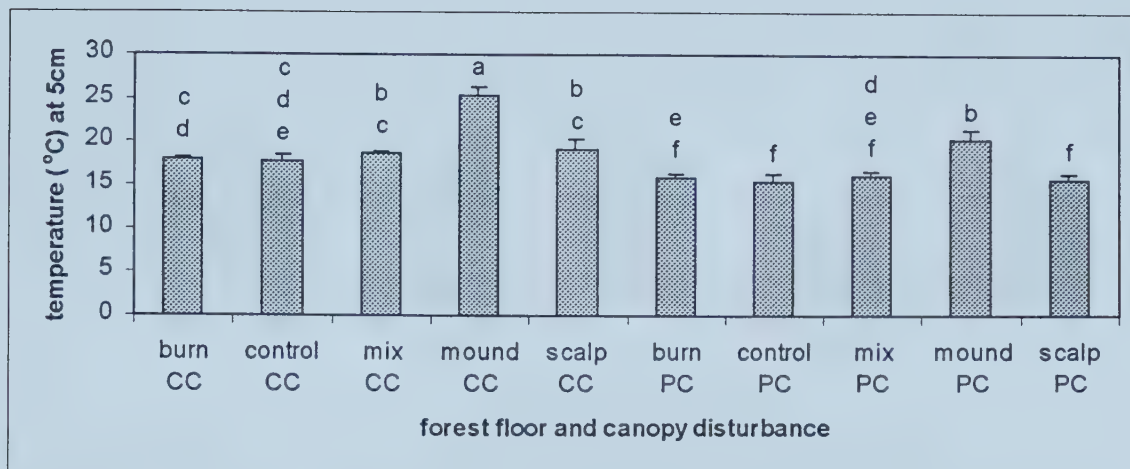
Figure 2.3. Soil temperature at 5cm depth in relation to forest floor disturbance and canopy removal (CC = clearcut and PC = partial cut). Average for mid-afternoon, clear day measurements in June, July, and August 1999. (mean ± SE, n = 3). Columns with the same letter are not significantly different.
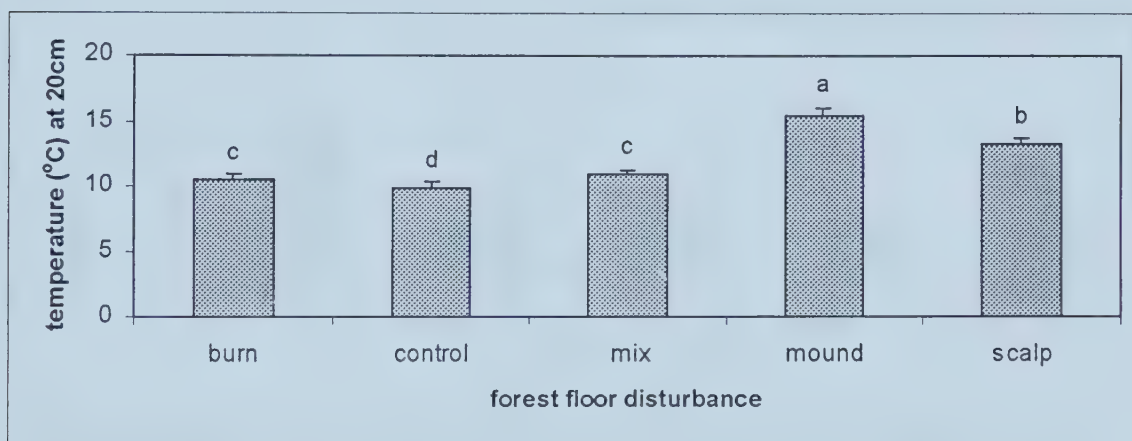

Figure 2.4. Soil temperature at 20cm depth in relation to forest floor disturbance. Average for mid-afternoon, clear day measurements in June, July, and August 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.

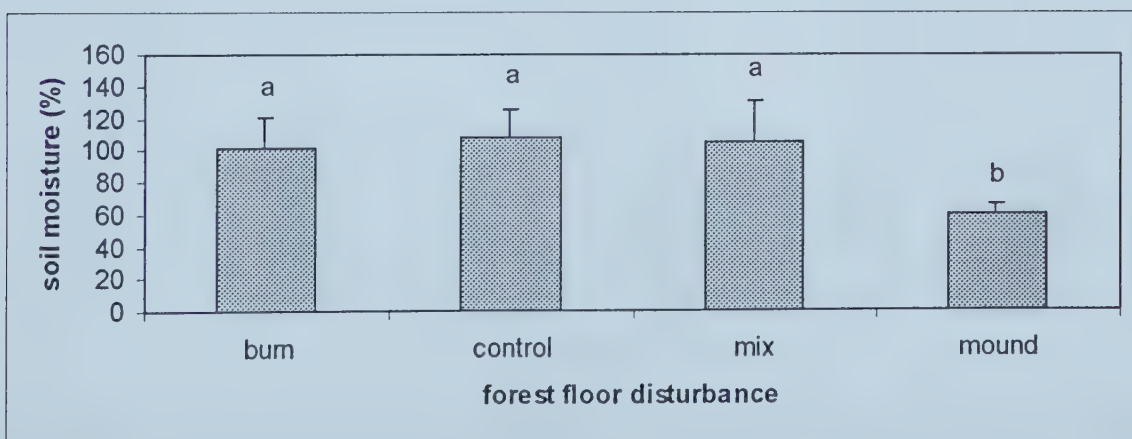Figure 2.5. Soil moisture in the organic horizon in relation to forest floor disturbance. Average for samples taken in July and August 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
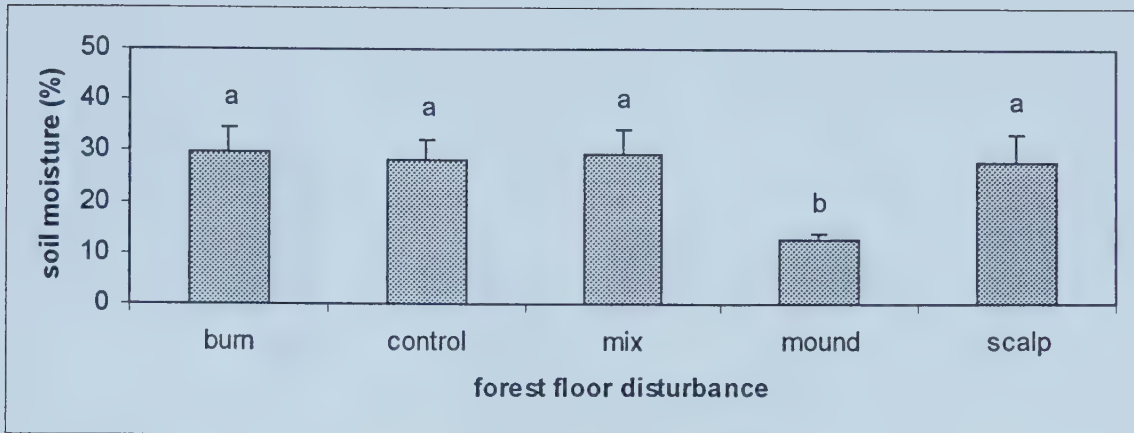
Figure 2.6. Soil moisture in the mineral horizon in relation to forest floor disturbance. Average for samples taken in July and August 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.

Figure 2.7. Ammonium (NH_4^+) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.

Figure 2.8. Nitrate (NO_3^-) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.

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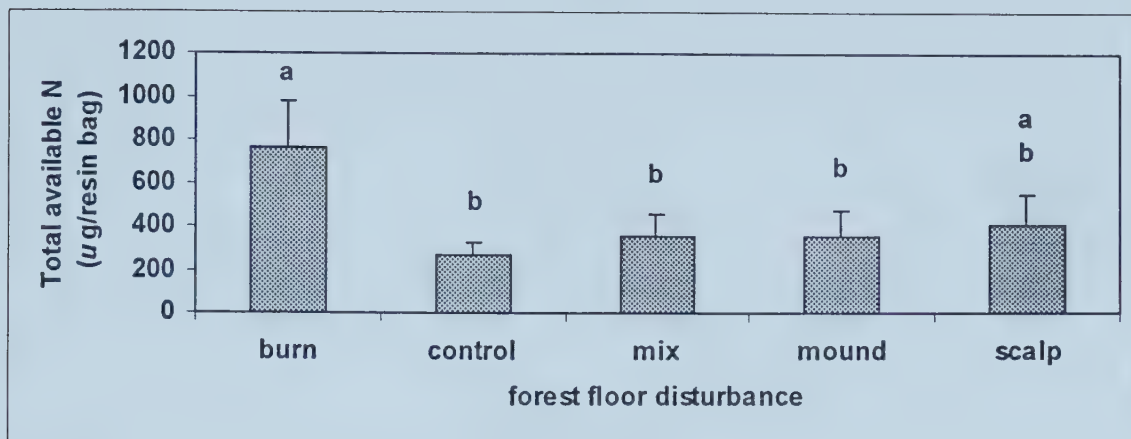
Figure 2.9. N availability ($NH_4^+ + NO_3^-$) in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
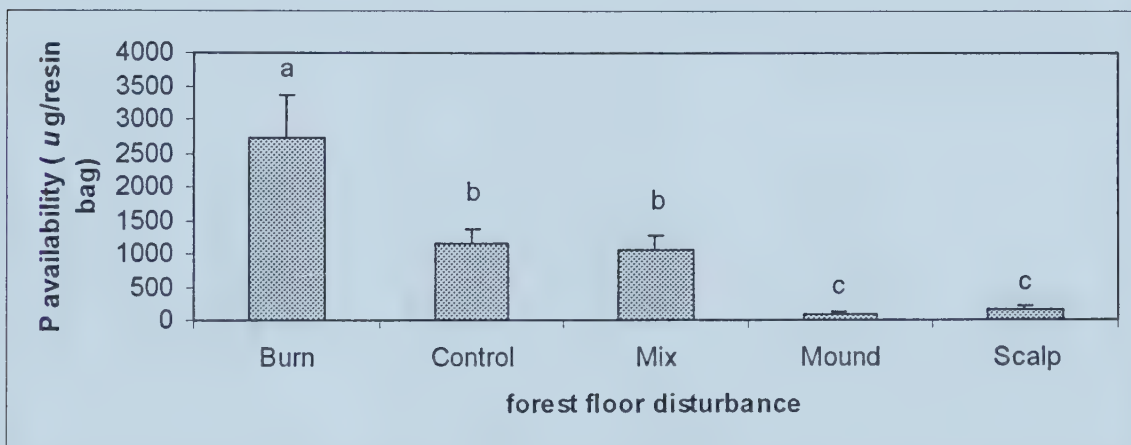
Figure 2.10. Phosphorous (P) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
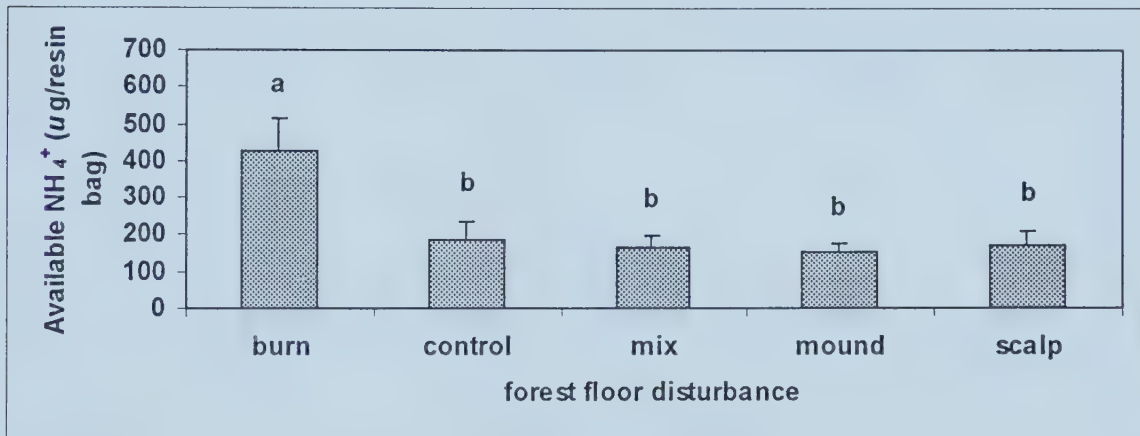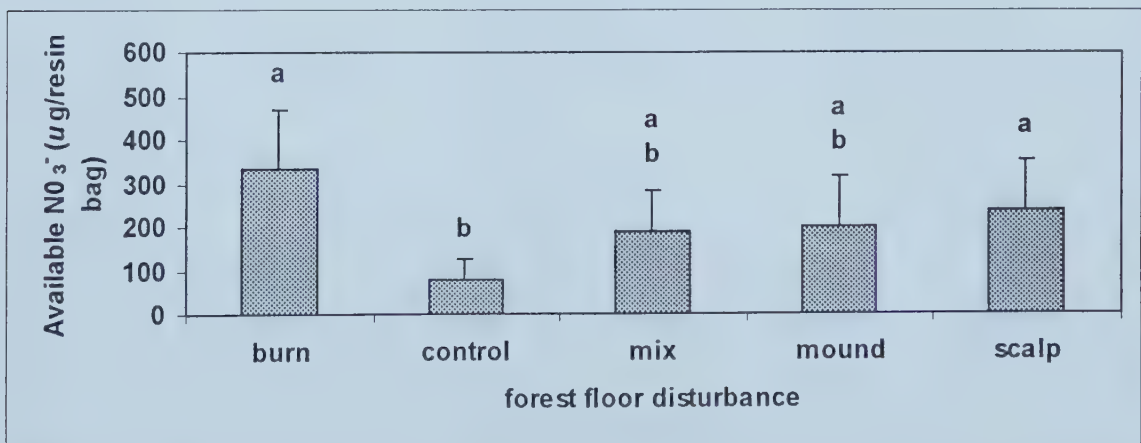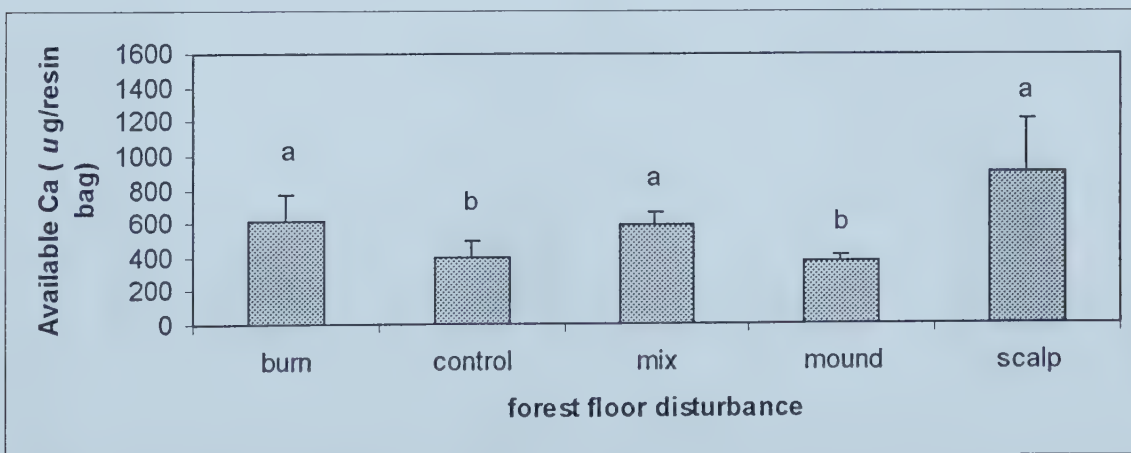

Figure 2.11. Calcium (Ca) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.

Figure 2.12. Magnesium (Mg) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
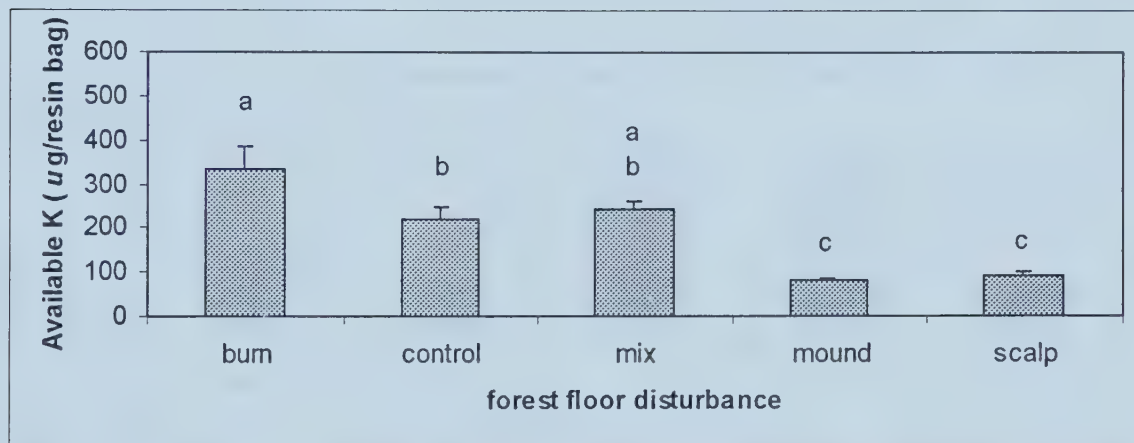
Figure 2.13. Potassium (K) availability in relation to forest floor disturbance as measured by resin bags for the period June – October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.


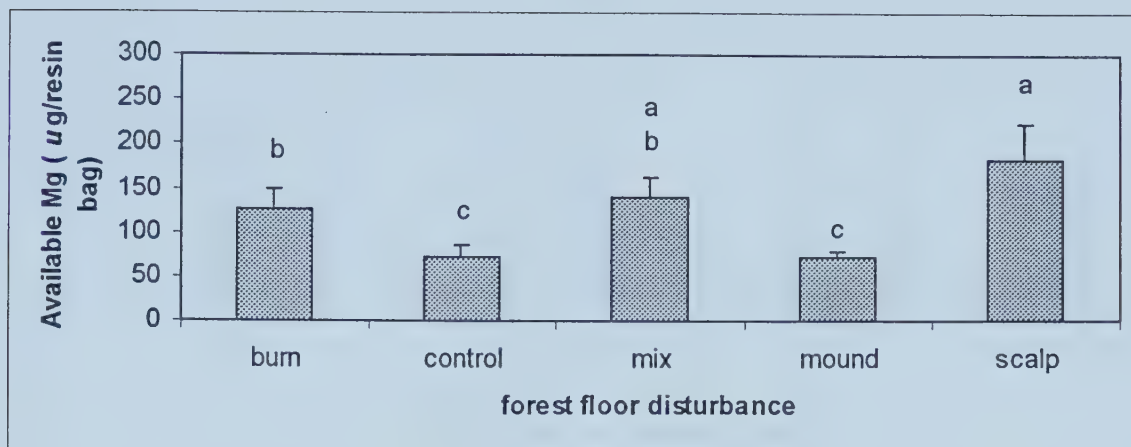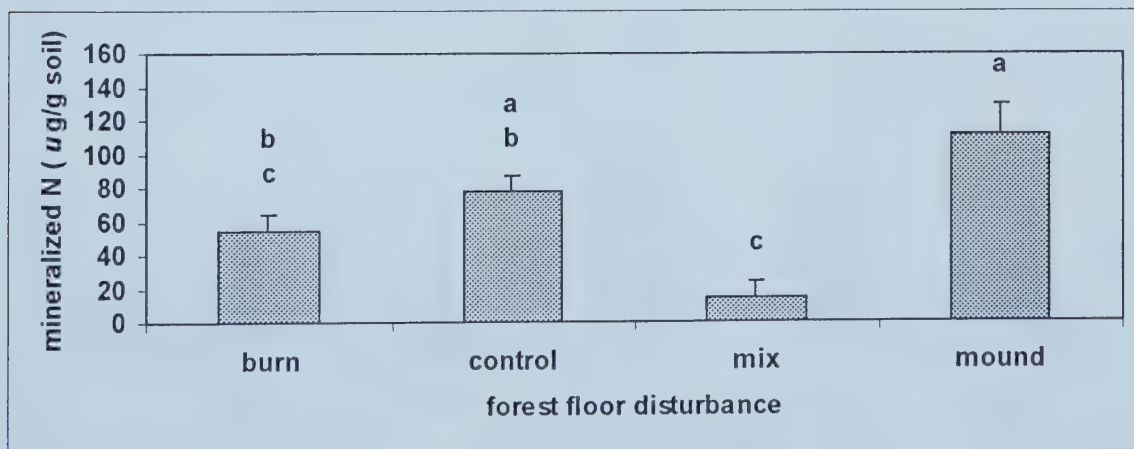
Figure 2.14. Net N mineralization in relation to forest floor disturbance as measured by in situ incubations of the organic horizon during July-October 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
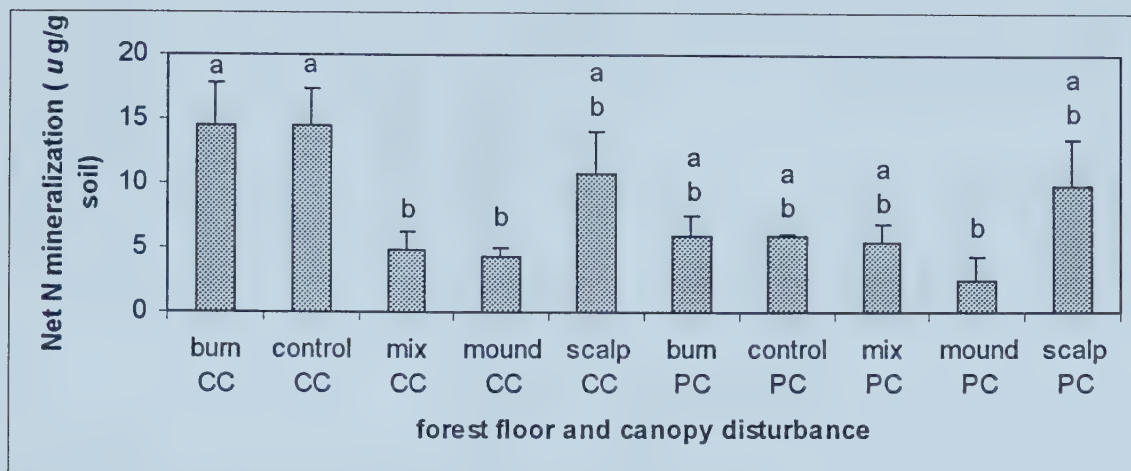
Figure 2.15. Net N mineralization in relation to forest floor disturbance and canopy removal (CC = clearcut and PC = partial cut) as measured by in situ incubations of the mineral horizon during July-October 1999. (mean ± SE, n = 3). Columns with the same letter are not significantly different.
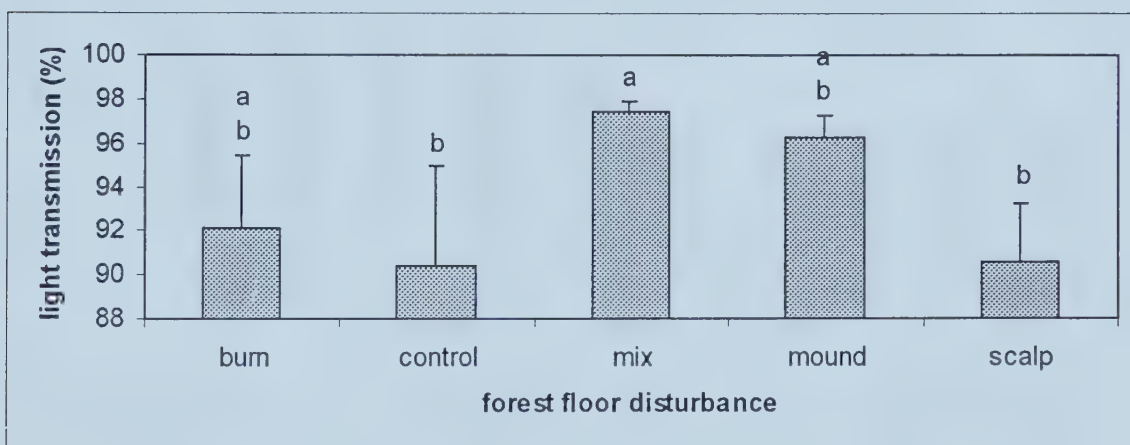
Figure 2.16. Light transmission to 30 cm height through the shrub/herb layer as percent of above shrub/herb light in each forest floor disturbance measured in August 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
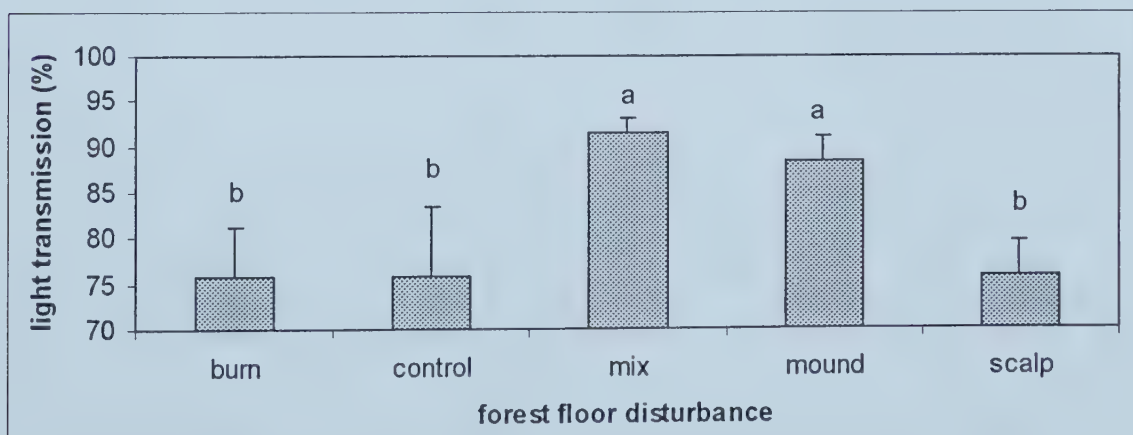
Figure 2.17. Light transmission to ground level through the shrub/herb layer as percent of above shrub/herb light in each forest floor disturbance measured in August 1999. (mean ± SE, n = 6). Columns with the same letter are not significantly different.
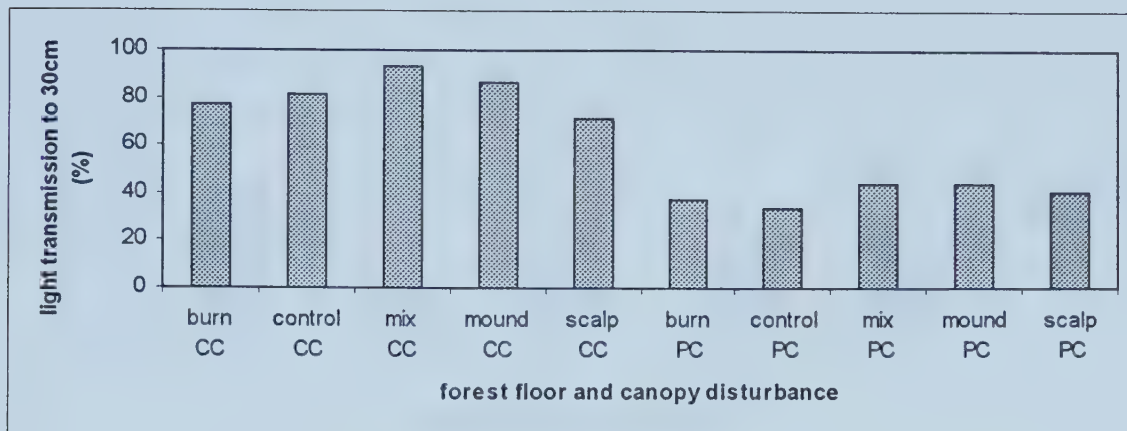
Figure 2.18. Actual light transmission to 30 cm height through the shrub/herb layer in each forest floor disturbance measured in August 1999. (mean only).
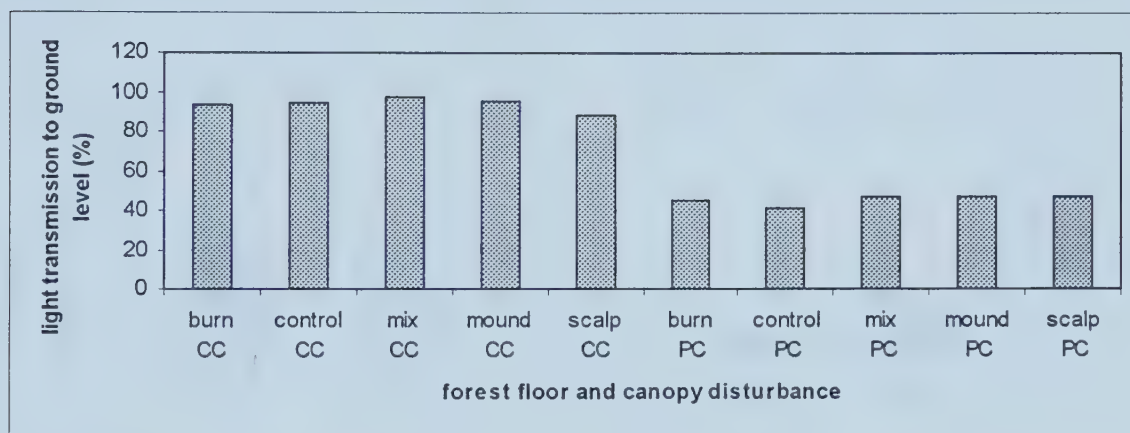
Figure 2.19. Actual light transmission to ground level through the shrub/herb layer in each forest floor disturbance measured in August 1999. (mean only).

Figure 2.20. Density of *E. angustifolium* in relation to forest floor disturbance as measured in 1999 (year 1). (mean ± SE, n = 6). Columns with the same letter are not significantly different.

Figure 2.21. Density of *V. edule* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.

Figure 2.22. Density of *R. acicularis* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
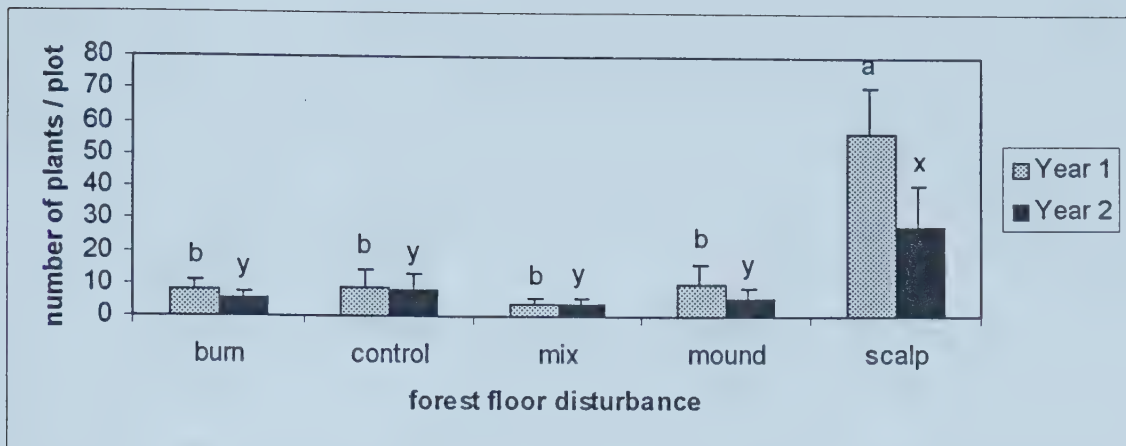
Figure 2.23. Density of *Populus* spp. in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
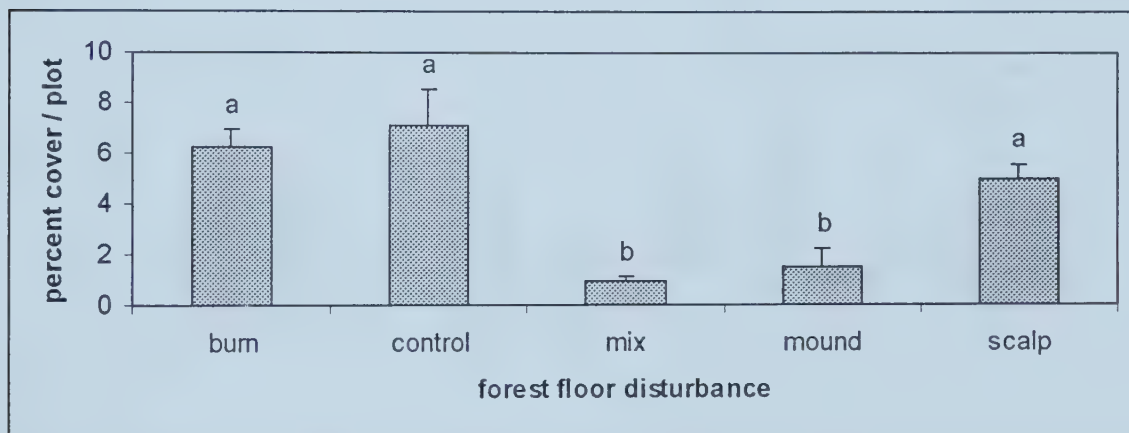
Figure 2.24. Total percent cover of all herbaceous species in relation to forest floor disturbance as measured in July 1999 (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
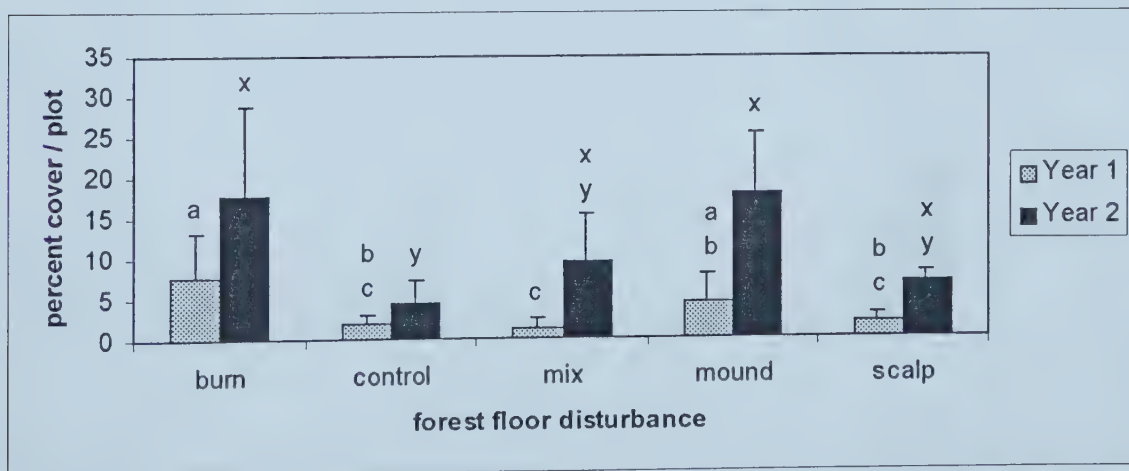
Figure 2.25. Percent cover of *E. angustifolium* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
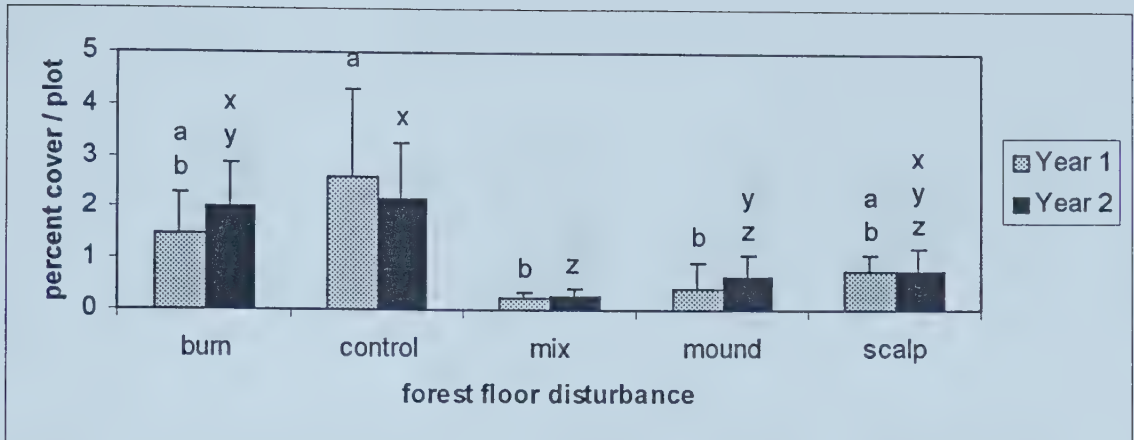
Figure 2.26. Percent cover of *V. edule* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
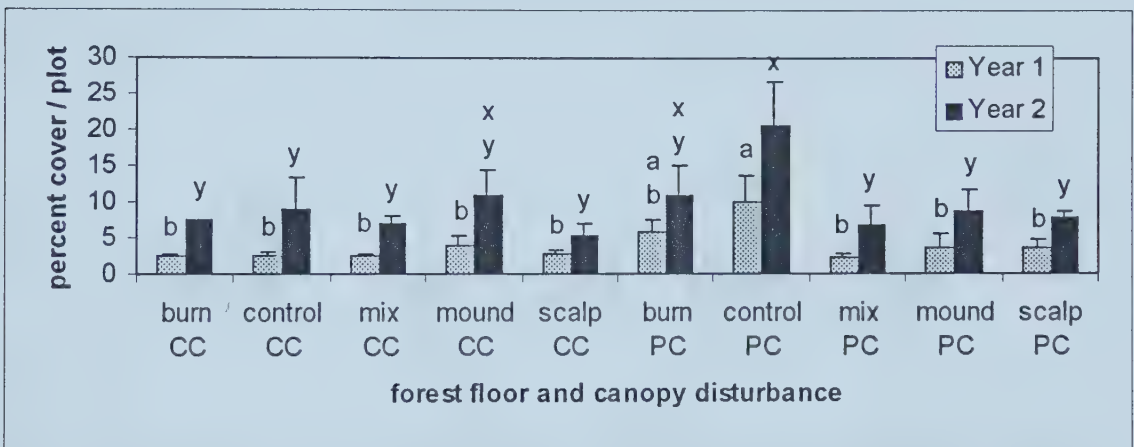
Figure 2.27. Percent cover of *R. acicularis* in relation to forest floor disturbance and canopy removal (CC = clearcut and PC = partial cut) as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 3). Columns with the same letter for the same year are not significantly different.
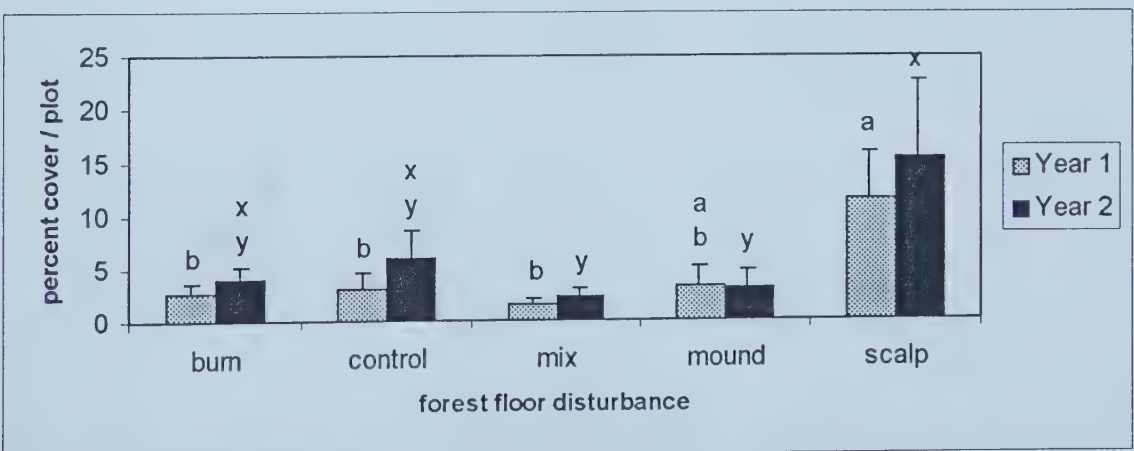
Figure 2.28. Percent cover of *Populus* spp. in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
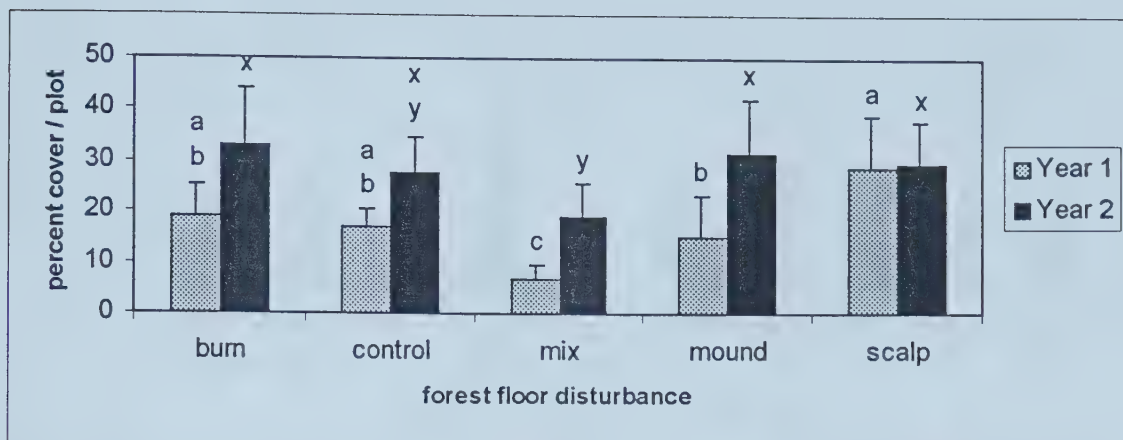
Figure 2.29. Combined percent cover of *E. angustifolium, V. edule, R. acicularis and Populus spp.* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n =6). Columns with the same letter for the same year are not significantly different.
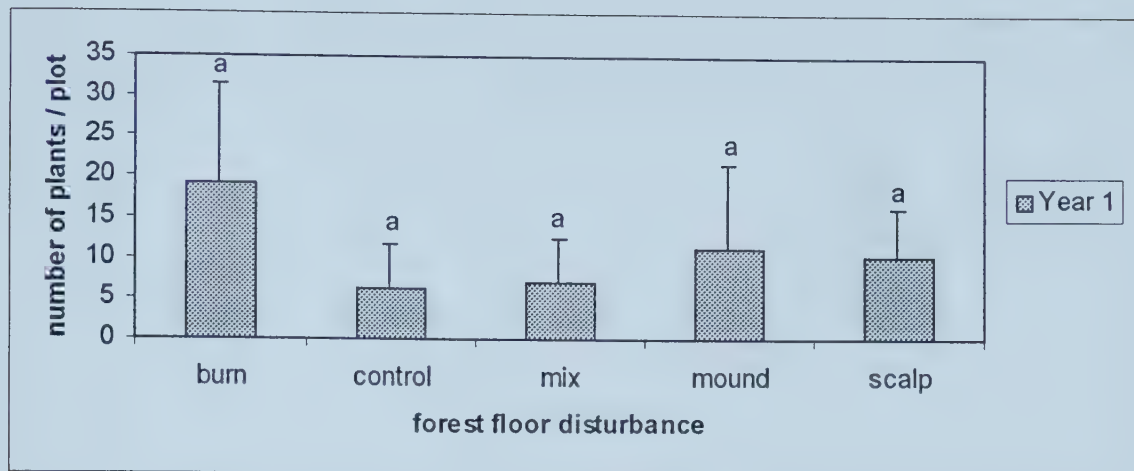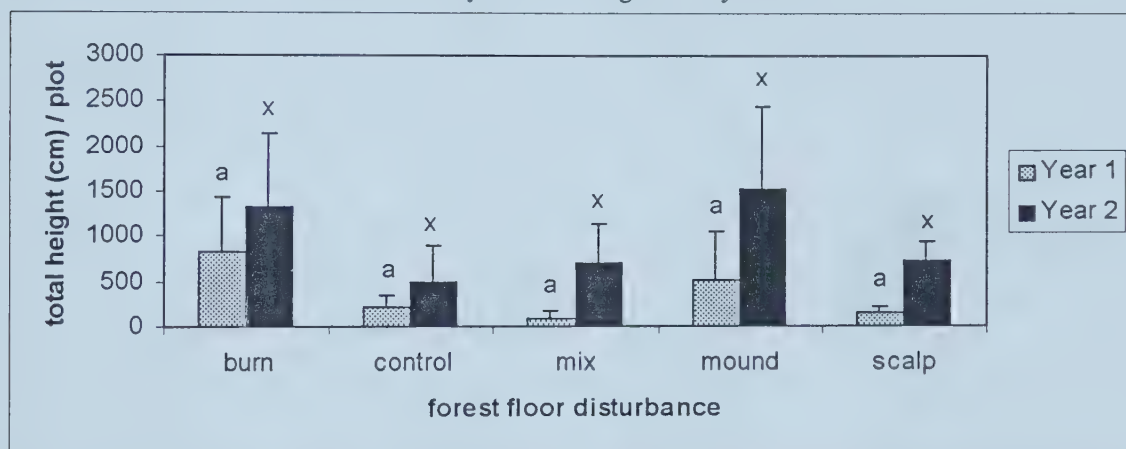

Figure 2.30. Total stem length of *E. angustifolium* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
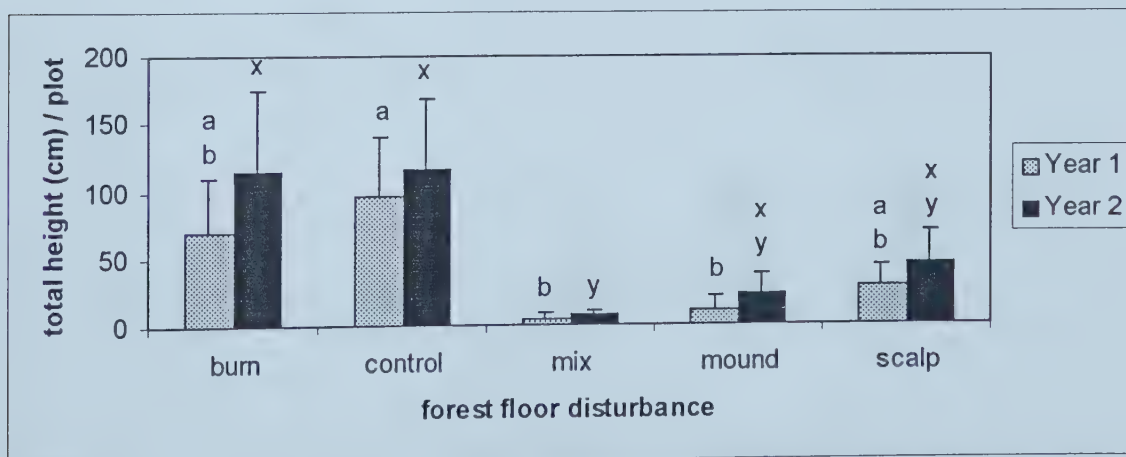
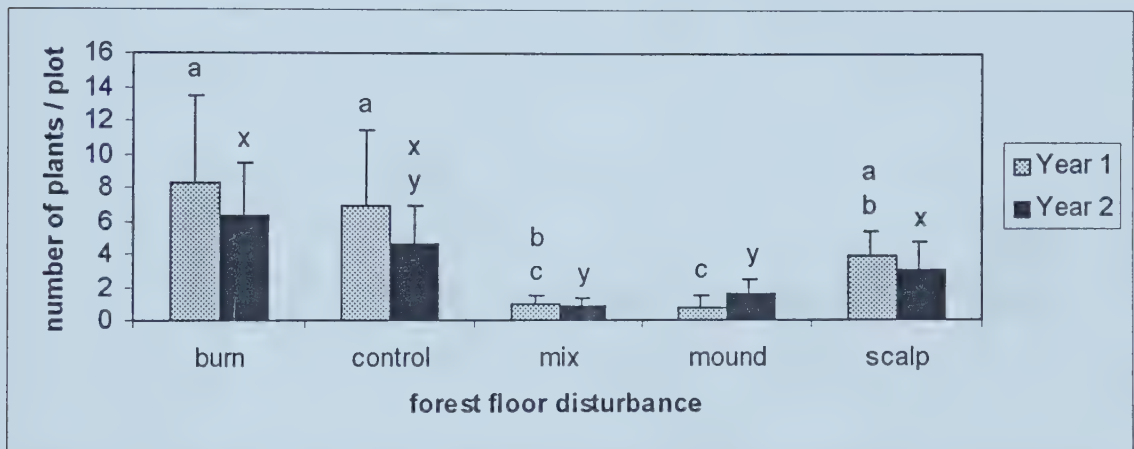Figure 2.31. Total stem length of *V. edule* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 3). Columns with the same letter for the same year are not significantly different.
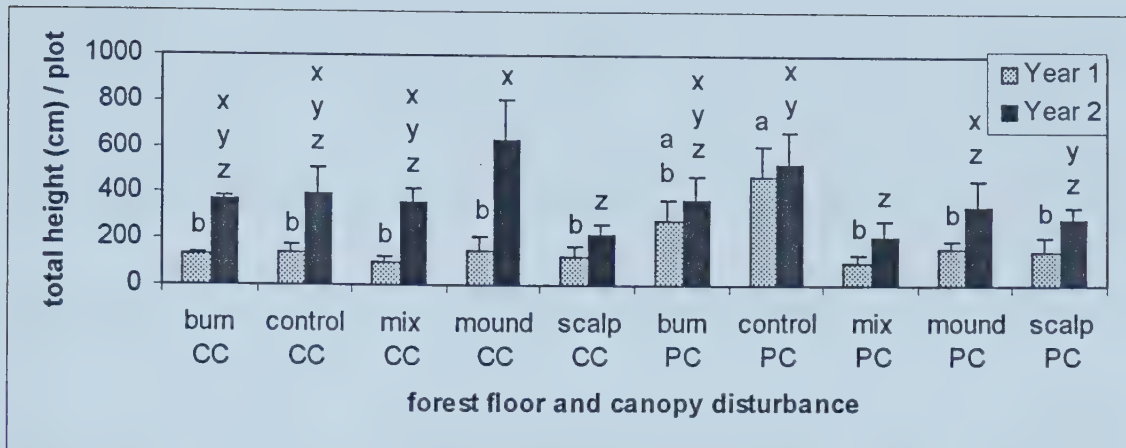
Figure 2.32. Total stem length of *R. acicularis* in relation to forest floor disturbance and canopy removal (CC = clearcut and PC = partial cut) as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 3). Columns with the same letter for the same year are not significantly different.
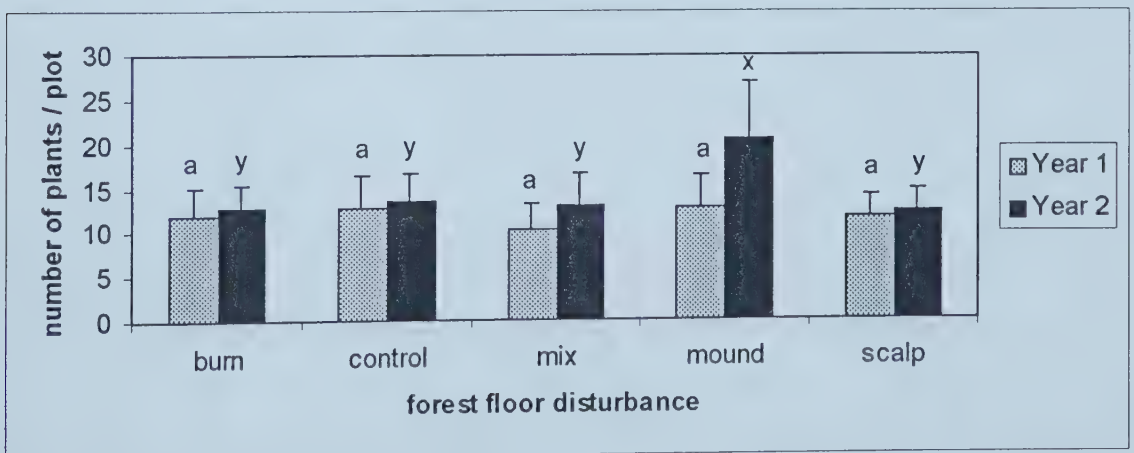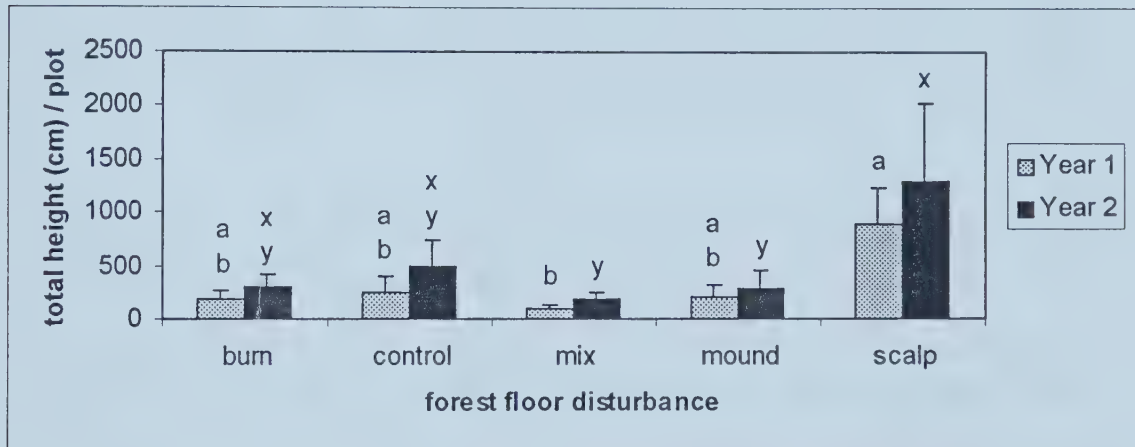

Figure 2.33. Total stem length of *Populus* spp. in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.
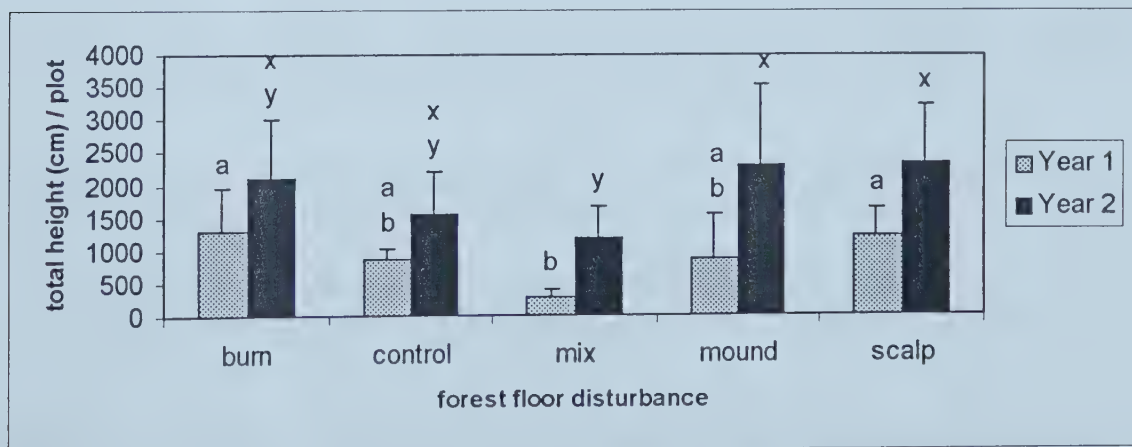
Figure 2.34. Combined total stem length of *E. angustifolium, V. edule, R. acicularis and Populus spp.* in relation to forest floor disturbance as measured in 1999 (year 1) and 2000 (year 2). (mean ± SE, n = 6). Columns with the same letter for the same year are not significantly different.

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Chapter 3. Loss of dominant shoot and availability of nitrogen as factors controlling sprouting in fireweed.

Introduction

Epilobium angustifolium L., commonly referred to as fireweed, is a widespread perennial forb found throughout the boreal forest. Fireweed is most abundant on recently disturbed sites, and is noted for its rapid colonization of burned areas following fire. Its ability to invade burned areas by seed is well established (Archibold 1980, Haeussler and Coates 1986). High intensity burns create favourable substrates for seedling establishment by reducing the forest floor and exposing mineral soil (Ahlgren 1960). Consequently, the highest cover and density of fireweed are typically observed on more severely burned areas (Ahlgren 1960, Bartos and Mueggler 1981, Dyrness and Norum 1983). Nonetheless, fireweed density has also been observed to be substantially lower on more severe burns than on moderate burns with less forest floor consumption (Anderson and Romme 1991). Vegetative regeneration predominates where fireweed clones are already established (Broderick 1990) and could be as important as regeneration by seed as a mechanism for establishment in burned areas. Indeed, where disturbance to the forest floor is moderate, roots and rhizomes of fireweed may avoid damage and sprout to recolonize a site (Haeussler and Coates 1986, Flinn and Wein 1977, McLean 1968, Kiil 1970).

Higher resource availability (light, temperature, nutrients) likely drives fireweed productivity, but the reasons for increased sprouting following low-intensity burns are not well understood. Higher soil temperatures, typically observed following fire, could be a possible stimulus for sprouting, however temperature increases in a low-intensity burn are small (Chapter 2) due to the limited reduction of the forest floor. Increased nitrogen availability following disturbance has been shown to stimulate sprouting of dormant buds in *Agropyron repens* (Qureshi and McIntyre 1979) and might also promote increased sprouting of fireweed. A further possibility, following from the work of Emery (1955), is that bud development is suppressed by high auxin levels. Destruction of the dominant emerging shoots by fire could release dormant buds from hormonal suppression and thus promote sprouting.

The study objectives were to determine mechanisms for increased sprouting by fireweed following fire. It was hypothesized that: (1) destruction of the emerging shoot results in the release of dormant buds and increased sprouting and/or (2) increased nutrient availability after burning stimulates increased sprouting.

Materials and Methods

The study site was located 30km east of Slave Lake, Alberta (55° 17' N 114° 46'W). Aspen (*Populus tremuloides* Michx)-dominated stands, with a small component of white spruce (*Picea glauca* [Moench] Voss), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) were clearcut during the winter of 1999/2000. In mid-May of 2000, 50 x 50 cm plots were established throughout the clearcut, each plot centred on a single fireweed sprout emerging from the soil. These were the first emerging sprouts of the year, and they were considered to be the dominant shoots (and buds). The experiment was a 2 x 3 factorial design with 2 levels of shoot removal (cut vs. uncut) and 3 levels of nitrogen addition (NH_4^+ vs. NO_3^- vs. no nitrogen). The shoot removal treatment involved cutting the emerging shoot at ground level. Nitrogen additions were achieved using $Ca(NO_3)_2$ as a NO_3^- source and $(NH_4)SO_4$ as a NH_4^+ source. Fertilizers were applied in a granulated form at a rate of 200 kg/ha to the surface of the 50 X 50 cm plot. All treatments were applied on the same day as plot installation. The experimental design was fully randomized, with 15 replicates of each treatment combination, for a total of 90 plots. Plots were randomly assigned to treatments, and the plots were dispersed widely throughout the 20 hectare clearcut.

Plots were destructively sampled in early September 2000. All fireweed plants in each plot were counted and heights were measured. Fireweed plants in each plot were then cut at ground level, bagged, and returned to the lab. Bags containing the plants from each plot were dried at 68°C for 48 hours to determine plant dry weight.

Data were log transformed where necessary to meet assumptions of normality and homogeneity of variance. The data were analyzed by analysis of variance (ANOVA) using the SAS (SAS Institute Inc. 1987) Proc GLM feature. The general model used was:

$$Y_{ij} = u + C_i + N_j + e_{ij}$$

where C is cutting treatment (i = 1 or 2) and N is the nitrogen addition (j = 1, 2 or 3). Significance was evaluated at the $p<0.05$ level.

Results

Removal of the emerging shoot by cutting significantly increased shoot density ($p=0.0471$; figure 3.1a), but there was no detectable effect of nitrogen addition. In contrast, biomass on a plot basis was strongly affected by nitrogen addition ($p<0.0001$; figure 3.2a), but not by cutting. Biomass on a per plant basis was higher with nitrogen addition ($p=0.0002$; figure 3.2b), but was lower when shoots were removed by cutting ($p=0.0232$; figure 3.1b). There were no significant interactions between cutting and nitrogen addition for any of the measured variables.

Discussion

Removal of the emerging shoots by cutting resulted in a higher shoot density. This suggests that the destruction of emerging shoots that occurs during a surface burn is at least partly responsible for increased sprouting following light spring fires. The physiological control of this response is not apparent from this study, but the release of dormant buds following shoot disturbance is common in other boreal plants such as *Calamagrostis canadensis* (Powelson and Lieffers 1991) and *Populus tremuloides* (Schier 1972). It is well established in *P. tremuloides* that stem removal interupts the flow of auxin, which suppresses bud development, thereby releasing buds to produce shoots (Schier 1972). Emery (1955) established that auxin had a role in suppressing bud formation on fireweed roots, so it is plausable that the sprouting response observed in this study may be related to the interruption of auxin.

While there are no reports of the response of fireweed to manual cutting (Comeau et al. 1989), other evidence suggests that removal of emerging shoots could stimulate sprouting. Increased sprouting has been observed following the grazing of fireweed (Ingram 1931), a surface-level removal treatment analogous to cutting or light burning. The vigorous sprouting response previously observed following low-intensity spring fires in Alberta (Kiil 1970, B. Frey personal observation) or following clearcutting (Haeussler

and Coates 1986) may be attributed to the destruction of the dominant shoot or its bud by disturbance at surface of the forest floor.

Given the small area of our study plots, it is likely that the new sprouts probably originated from buds at the base of the cut stem or the adjoining roots. Repeated sprouting and die-back in conjunction with the formation of new buds below the stump of the former shoot results in a proliferation of buds at the stem base (Moss 1936). Furthermore, buds can be formed rapidly on excised roots days after cutting (Emery 1955). Proliferation of shoots from a single stem base may explain in part the clumping pattern of fireweed that has been observed during invasion of disturbed sites (Comeau et al. 1989).

In spite of greater shoot density following cutting, overall biomass production was not increased by cutting, but was increased by nutrient addition. Fireweed has a relatively high nutrient uptake per unit of biomass (Dyrness and Norum 1983, van Andel and Vera 1977). The fact that increased shoot density did not promote increased aboveground biomass suggests that biomass production in the cut and unfertilized plots was limited by nutrients. Indeed, on a biomass per plant basis, it was clear that fertilized plants were heavier, while cutting the dominant sprout probably resulted in an overall decline of resources for the clone, despite the eventual great number of stems. It was also possible that the delayed development of fireweed in the cutting treatment allowed other vegetation to establish, thus reducing the overall growth of sprouts in the plot.

Though sprouting was clearly increased by cutting, it is surprising that the differences were not more substantial. Following a recent burn in Alberta, excavated fireweed stem bases were found to have numerous sprouts initiating from the stem base of fire-killed shoots (B. Frey, personal observation). There are a number of possible explanations for the limited increase in sprouting in this study. First, it is possible that more sprouts emerged on the cut plots than were evident at the final sampling time. Competition between sprouts, self-thinning and reestablishment of dominants may have reduced the final shoot density. Second, it is quite likely that other dominant shoots (i.e. shoots that would develop in the absence of the treatments) emerged after the installation of the study, and could possibly have limited the sprouting response by suppressing lateral buds. Third, given that fireweed clones can cover distances of many metres

(Broderick 1980), it is possible that shoots outside the plot, but of the same clone, could have suppressed sprouting. I only removed one sprout by cutting, whereas there may have been many more shoots on the same clone but outside the plot. Perhaps the removal of more dominant shoots over a wider area, as would happen with a burn, would promote a more vigorous sprouting response.

In summary, destruction of the dominant shoot stimulated sprouting of fireweed, which may explain, at least in part, the increased sprouting observed following low-intensity burns. Increased nitrogen availability, as is commonly observed following fire, did not appear to increase sprouting but resulted in greater biomass. No interaction between nitrogen addition and cutting was evident. An adaptation of increased sprouting following low-intensity burns (where substrates are not favourable to regeneration by seed) should allow fireweed to take full advantage of increased resource availability and thus increase its dominance on a site following fire. Consequently, increased sprouting in conjunction with increased biomass production may allow fireweed to vigorously colonize low-intensity burns.
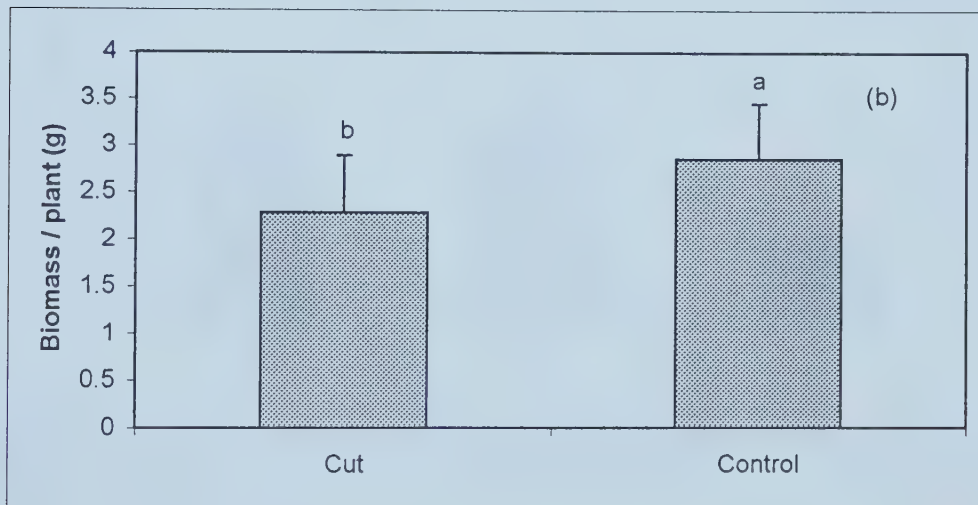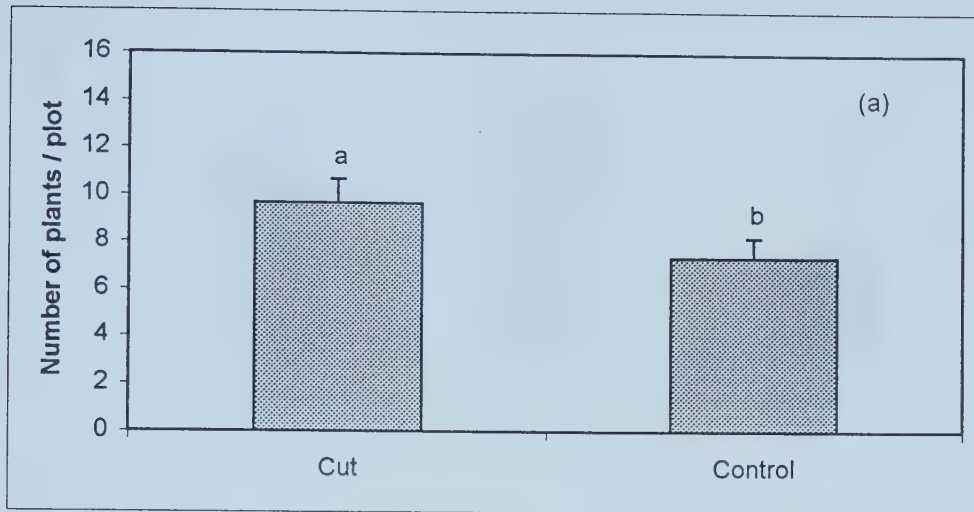
Figure 3.1(a). Mean shoot density per plot as affected by stem removal through cutting. (b) Mean per plant biomass as affected by stem removal through cutting. Bars sharing the same letters are not significantly different (mean±SE, n=45).
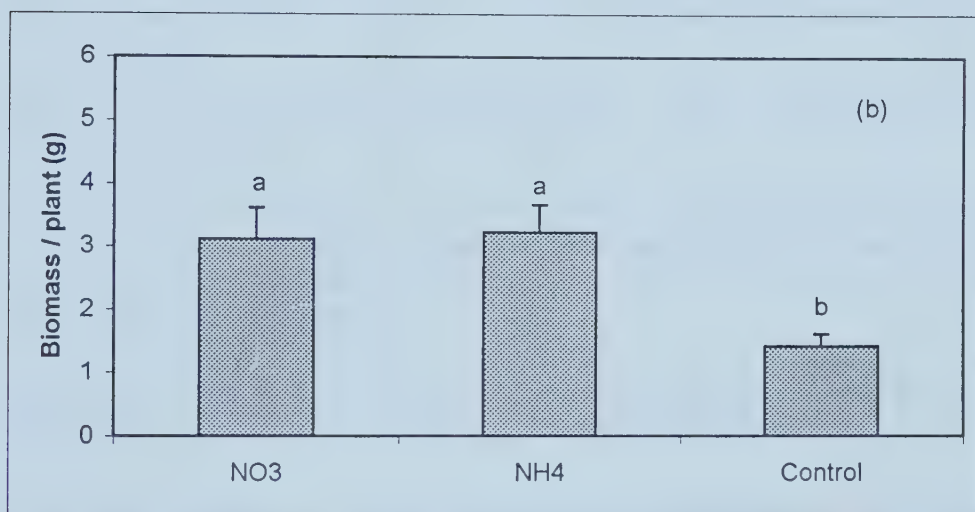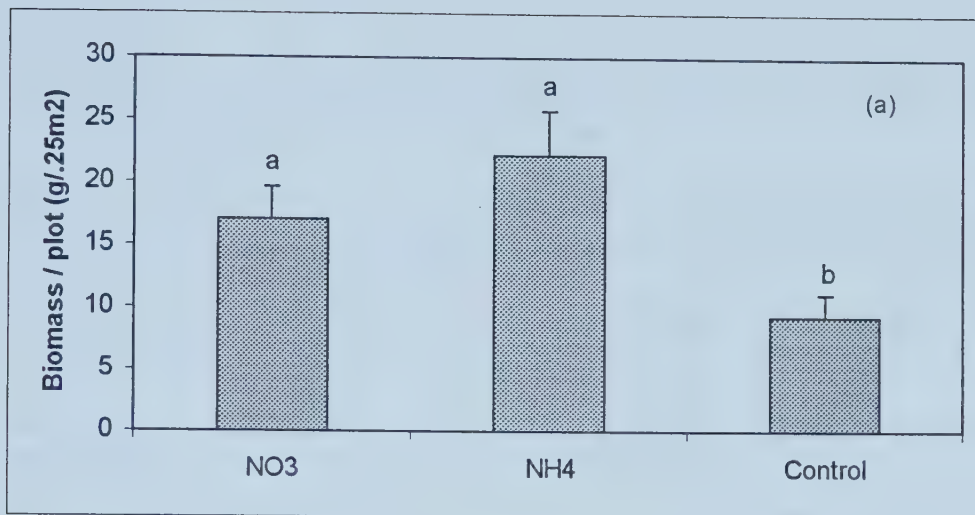
Figure 3.2 (a). Mean plot-level fireweed biomass as affected by nitrogen additions. (b) Mean per plant biomass as affected by nitrogen additions. Bars sharing the same letter are not significantly different. (mean±SE, n=45).

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Chapter 4 – Summary of findings, management implications and future research

Summary

The overall objective of this study was to evaluate the responses of different competing vegetation species to site preparation and canopy disturbance, with a view to assessing the suitability of different types of disturbances for the establishment of planted white spruce. The first study evaluated the interactive effects of harvest type (clearcut-CC or partial cut-PC) and forest floor disturbance (burning, mixing, mounding and scalping) on vegetation and nutrient dynamics. As expected, there were significant impacts of the treatments on environmental variables, nutrient dynamics and vegetation response. Soil temperatures were higher in the CC than in the PC, and temperatures in forest floor treatments were generally in the order mound > scalp > mix > burn > control. Soil moisture in both organic and mineral horizons did not appear to differ between harvest levels, but soil moisture was reduced in both the mineral and organic layers of the mound compared to the other forest floor treatments.

In terms of nutrient availability, there was higher Mg, and a trend to higher Ca, in the CC than in the PC, but otherwise there was no clear impact of harvest type on either nutrient availability or mineralization rates. In contrast, forest floor treatments substantially altered nutrient availability. Burning resulted in the highest availability of NH_4^+, NO_3^-, and P, while control plots had the lowest NO_3^- availability. Calcium and Mg availability were highest in the scalping treatment, while K availability was the lowest in the scalp. Net N mineralization in the organic layer was highest in the mounding treatment, and lowest in the mixing treatment. No clear trends were apparent for N mineralization in the mineral soil cores.

Vegetation response was evaluated by measuring percent cover and height for *Viburnum edule, Rosa acicularis, Populus* spp. and *Epilobium angustifolium*. The responses showed that different types of disturbance promoted different vegetation. Burning promoted higher cover of *E. angustifolium*, while scalping promoted root suckering by *Populus* spp. Vegetation response in mounds was highly variable, with some mounds being colonized vigorously while others were relatively uncolonized.

Mixing reduced vegetation establishment to the greatest degree, and thus provided the best control of competing vegetation.

In the second study (chapter 3), destruction of the dominant shoot of *E. angustifolium* stimulated an increase in sprouting. This effect may explain, at least in part, the increased sprouting observed following low-intensity burns. Increased nitrogen availability, as is commonly observed following fire, did not appear to increase sprouting but resulted in greater aboveground biomass. Increased sprouting by *E. angustifolium* following low-intensity burns (where substrates are not favourable to regeneration by seed) may allow it to establish rapidly and increase its dominance following fire.

Study limitations

This study was not able to detect a clear effect of canopy retention on nutrient and vegetation dynamics. It was not clear whether this was a function of inadequate replication and site variability, whether there was no effect, or whether differences were simply not evident at this time after disturbance. Other studies evaluating the effects of partial harvesting or thinning on decomposition and nutrient dynamics have not found clear trends. In balsam fir stands, thinning has been shown to increase nutrient availability (Thibodeau et al. 2000) while in white pine stands thinning had little effect on nutrient availability (Burgess and Wetzel 2000). Prescott (1997) found differences in decomposition and nitrogen mineralization between mature unharvested stands and stands harvested at various intensities, but did not find differences among the different harvest levels. It may be that differences are only evident when comparisons are made with undisturbed stands. Any level of harvesting involves some disturbance and this disturbance, especially at ground level, may have significant effects on soil processes (Prescott 1997). As a consequence, differences between different harvest levels may be smaller than comparisons with unharvested stands. Microclimatic conditions may be less different among different harvest levels compared with uncut stands (Prescott 1997). A further complication is high spatial variability in nutrients within replicates, which can be much larger than differences associated with cutting-level (Maynard et al. 1998), thus making efforts to identify any potential difference difficult. Lastly, vegetation may be a more important sink than microbial biomass in disturbed patches (Bauhus and Barthel

1995).   Given that vegetation response was similar in both cutting treatments in this study, nutrient availability may have reflected that similarity.

I also expected to observe a greater influence of canopy retention on understorey vegetation. Cover and height of early successional species are generally reduced at the lower light levels found under a canopy (Lieffers and Stadt 1994).   The lack of an effect of canopy in my study may be attributed to differential impacts of CC and PC harvest on shrub survival.   In the CC plants had to resprout from stored reserves, whereas in the PC many shrubs escaped damaged, and this may have obscured any differences. Consequently, there may be a time lag before the effect of canopy retention on vegetation is expressed (Thomas et al. 1999). Other studies suggest that vegetation may be slow to respond to canopy removal. In Australia, understory cover in a Eucalypt stand had not changed 6 years after thinning (Bauhus et al. 2001). In Washington, thinning had little effect on vegetation cover after 27 years (He and Barclay 2000).

This study could also have been more mechanistic in its approach to understanding vegetation dynamics in response to disturbance. Studies of disturbance, particularly of site preparation, need to be more mechanistic and focus on regeneration properties if dynamics of competing vegetation are to be better understood (Mallik et al. 1997). This is especially true for clonal species as their distribution predisturbance presence will affect the extent of vegetative regeneration.   This study was weakened by the lack of knowledge of the predisturbance vegetation in the experimental area which would have provided a baseline for understanding clonal response. More mechanistic studies such as Landhäusser and Lieffers (1999) are needed.

Management Implications

The main objective of silvicultural treatments at the forest floor level or at canopy level are to improve the conditions for the establishment of planted white spruce seedlings. Forest floor treatments, including mechanical site preparation or prescribed burning, can be used to improve tree seedling microclimate, increase nutrient availability and control competing vegetation (Örlander et al. 1990). Partial canopy retention can provide more optimal understory climate conditions for tree seedlings and limit light to

the understory to minimize the development of competing vegetation (Man and Lieffers 1999, Lieffers and Stadt 1994).

The treatments assessed in this study included combinations of harvest type (CC vs. PC) and different forest floor disturbances, with a specific focus on nutrient and vegetation responses. In general, the results show that different types of disturbance at the forest floor level will have different impacts on nutrient availability and vegetation development.   Vegetation control is especially critical to tree seedling establishment, therefore treatments which control vegetation are expected to be the most suitable for white spruce seedlings. Nutrient availability will also be important, however high nutrient availability following disturbance can be of more benefit to competing vegetation (Thevathasan et al. 2000). Consequently, high nutrient availability induced by the disturbance may not benefit the tree seedling in the short term, or may even be detrimental if it increases competition or results in leaching losses.   In terms of the application of these research findings, I would anticipate that other mesic, white-spruce dominated stands on similar soils and with similar plant species composition found throughout the boreal mixedwood of Alberta would respond in a similar way. With this in mind, the following management implications are presented:

1. **Nutrient management**. All the forest floor disturbances increase the availability of at least some nutrients, and generally increase N mineralization. Elevated nutrient availability in the short-term will not be of much benefit to tree seedlings, but may stimulate greater cover of competing vegetation and or result in higher leaching losses. The mixing treatment substantially reduces N mineralization, suggesting it is the most preferable treatment for managing nutrient supply in the short-term.

2. **Suppression of vegetation**. The greatest suppression of vegetation may be obtained by a mixing treatment, likely because this treatment destroys the majority of sprouting organs. Mounds may also provide good suppression, but mounds on some sites may be vigorously colonized, suggesting a thicker mineral cap may be needed. Limiting vegetation establishment will ensure tree seedling access to light, nutrients and moisture and reduce the potential for snow press.

3. **Aspen regeneration and scalping**. Scalps which remove most of the forest floor appear to stimulate vigorous root suckering by *Populus* spp. Scalping is thus highly suitable for regenerating aspen, but will not likely be suitable for white spruce.

4. ***E. angustifolium* establishment and prescribed burning**. Vegetative establishment of *E. angustifolium* may be promoted by a low-intensity burn, and this may be favourable if it limits establishment by more vigorous competitors. *E. angustifolium* competes with white spruce, but is generally less aggressive than other competitors, such as *C. canadensis*.

5. **Partial cutting and vegetation control**. Canopy retention in a partial cut limits light transmission to the understory relative to a clear cut, and may reduce the vigour of competing vegetation. The growth and cover of *Populus* spp. is lower in a partial cut than in a clear cut, and this trend should follow for other competitors over the longer term. This should ensure more optimal growing conditions for white spruce.

Further Research

Further research should focus on several key areas, as follows:

1. **Disturbance studies with a mechanistic focus**. Studies should focus on understanding what drives the response (i.e. why did it happen?), rather than simply documenting the response as is often done with studies of site preparation. This requires a careful assessment of the disturbance depths of different treatments, depths of regenerative organs and depth of forest floor. Furthermore, where clonal regeneration is important, as in the boreal forest, a clear understanding of predisturbance vegetation is necessary. Considering this, further studies assessing the impacts of different mound size or mineral-cap thickness, mixing depth or depth of burn, could yield better insight into the factors controlling vegetation and nutrient dynamics.

2. **Rooting activity and uptake by retention trees**. It was not clear if rooting activity in the PC-forest floor treatment plots was diminished by disturbance. Lack of root development in the disturbance plots of the PC would limit uptake by retention trees, and could explain why nutrient availability did not appear lower in the PC compared

to the CC. Understanding how roots establish in such understory forest floor disturbance treatments would be of interest, both for understanding their contribution to patterns of nutrient availability in partial-cut systems and for evaluating the nutritional consequences of retention-tree nutrient uptake on understory-planted tree seedlings.

3. **Longer-term monitoring and assessment of vegetation and nutrient dynamics**. While no clear effects of canopy retention were evident in the short-term, differences are likely to become more pronounced with time as the lower light conditions constrain productivity of understory vegetation. Furthermore, if nutrient uptake by retention trees increases post-disturbance, diminishing nutrient availability (relative to the CC) may also constrain understory productivity.

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Impact of forest floor disturbance on first and second year shoot density of *E. angustifolium*, *V. edule*, *R. acicularis* and *Populus* spp.. Standard error of the mean given in parentheses. Means followed by the same letter are not significantly different (P<0.10) among forest floor disturbances for a given species.

	Burn	Control	Mix	Mound	Scalp
YEAR 1					
E. angustifolium	19 (12.4)*a*	6.3 (5.4) *a*	6.9 (5.4) *a*	11.3 (10.3) *a*	10.2 (5.9) *a*
V. edule	8.2 (5.3) *a*	6.9 (4.5) *a*	1 (0.5) *bc*	0.8 (0.7) *c*	3.9 (1.5) *ab*
R. acicularis	11.9 (3.2) *a*	12.9 (3.5) *a*	10.4 (2.9) *a*	12.9 (3.7) *a*	11.7 (2.4) *a*
Populus spp.	7.8 (3.3) *b*	8.6 (5.7) *b*	3.9 (1.5) *b*	10 (6.1) *b*	56.4 (14.5) *a*
YEAR 2					
E. angustifolium	43 (24.4) *a*	16 (13.9) *a*	23.6 (13.4) *a*	37.7 (26.9) *a*	31.2 (9.1) *a*
V. edule	6.3 (3.2) *a*	4.7 (2.3) *ab*	0.9 (0.4) *b*	1.5 (0.8) *b*	3 (1.7) *ab*
R. acicularis	12.8 (2.6) *b*	13.4 (3.3) *b*	13.2 (3.6) *b*	20.6 (6.3) *a*	12.3 (2.7) *b*
Populus spp.	5.7 (1.9) *b*	8.2 (4.7) *b*	3.9 (1.4) *b*	5.7 (3) *b*	27.5 (12.9) *a*

Appendix B

Impact of forest floor disturbance on first and second year cover of *E. angustifolium, V. edule, Populus* spp. and *R. acicularis* (note interaction with canopy disturbance for *R. acicularis*). Standard error of the mean given in parentheses. Means followed by the same letter are not significantly different (P<0.10) among forest floor disturbances for a given species. CC = clearcut and PC = partial cut.

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
YEAR 1					
E. angustifolium	7.8 (5.4) *a*	2 (1.1) *bc*	1.3 (1.2) *c*	4.4 (3.5) *ab*	1.9 (1) *bc*
V. edule	1.5 (0.8) *ab*	2.6 (1.7) *a*	0.3 (0.1) *b*	0.4 (0.5) *b*	0.8 (0.3) *ab*
Populus. spp.	2.6 (1) *b*	3 (1.6) *b*	1.5 (0.7) *b*	3.2 (2) *b*	11.5 (4.5) *a*

	CC-BR	PC-BR	CC-CT	PC-CT	CC-MX	PC-MX	CC-MD	PC-MD	CC-SC	PC-SC
R. acicularis	2.6 *b* (0.3)	5.8 *ab* (1.6)	2.5 *b* (0.7)	10.1 *a* (3.5)	2.4 *b* (0.3)	2.2 *b* (0.6)	3.9 *b* (1.4)	3.5 *b* (1.9)	2.7 *b* (0.7)	3.7 *b* (0.9)

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
Total	18.7 (6.6) *ab*	16.9 (3.7) *ab*	6.7 (2.7) *c*	15 (8.1) *b*	28.9 (10) *a*
YEAR 2					
E. angustifolium	17.9 (10.9) *a*	4.6 (2.8) *b*	9.6 (6) *ab*	17.9 (7.5) *a*	6.9 (1.4) *ab*
V. edule	2 (0.9) *ab*	2.2 (1.1) *a*	0.3 (0.1) *c*	0.6 (0.4) *bc*	0.8 (0.4) *abc*
Populus spp.	4 (1.3) *ab*	5.9 (2.7) *ab*	2.4 (0.7) *b*	3.1 (1.7) *b*	15.5 (7.3) *a*

	CC-BR	PC-BR	CC-CT	PC-CT	CC-MX	PC-MX	CC-MD	PC-MD	CC-SC	PC-SC
R. acicularis	7.4 *b* (0.2)	10.8 *ab* (4.2)	8.9 *b* (4.5)	20.6 *a* (6.1)	7 *b* (1.2)	6.6 *b* (2.9)	10.9 *ab* (3.6)	8.7 *b* (3.1)	5.3 *b* (1.6)	7.7 *b* (1)

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
Total	33 (11.2) *a*	27.4 (7.4) *ab*	19 (6.6) *b*	31.4 (10.6) *a*	29.7 (8.2) *a*

Appendix C

Impact of forest floor disturbance on first and second year total stem length of *E. angustifolium*, *V. edule*, *Populus* spp. and *R. acicularis* (note interaction with canopy disturbance for *R. acicularis*). Standard error of the mean given in parentheses. Means followed by the same letter are not significantly different (P<0.10) among forest floor disturbances for a given species. CC = clearcut and PC = partial cut.

YEAR 1

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
E. angustifolium	828 (603.7) a	213.8 (129.2) a	76.5 (84.7) a	507.7 (544.4) a	140.5 (81.5) a
V. edule	68.6 (40.5) ab	95.8 (44.7) a	4.9 (3.8) b	10 (11.6) b	29 (15.1) ab
Populus spp.	196.6 (74.5) ab	243.8 (158.2) ab	89.8 (48.2) b	205.1 (119.8) ab	888.9 (350.4) a

R. acicularis	CC-BR	PC-BR	CC-CT	PC-CT	CC-MX	PC-MX	CC-MD	PC-MD	CC-SC	PC-SC
	129.3b	276.7ab	140.2b	472.8	92.9b	96b	148.3b	154.3b	125.2b	149.3b
	(9.6)	(95.2)	(37.5)	(130.2)	(27.1)	(32.5)	(60.7)	(40.9)	(38.1)	(57.6)

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
Total	1296.3 (666.6) a	860 (167.7) ab	265.5 (134.2) b	874.2 (677.1) ab	1195.6 (432.8) a

YEAR 2

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
E. angustifolium	1321.5 (811.1) a	492.4 (399.4) a	715.8 (430.1) a	1516.2 (936.3) a	738.5 (196.3) a
V. edule	113.8 (61) a	115.4 (53.7) a	7.2 (4.1) b	22.4 (15.9) a b	45 (24.6) a b
Populus spp.	303 (105.1) ab	485.4 (252.3) ab	180 (65.3) b	283.7 (175.6) b	1293 (737.3) a

R. acicularis	CC-BR	PC-BR	CC-CT	PC-CT	CC-MX	PC-MX	CC-MD	PC-MD	CC-SC	PC-SC
	370.6 abc	364.3 abc	398.9 abc	524.2 ab	360.3 abc	211.3 c	632.5 a	338.8 ac	221.4 c	293.2 bc
	(12.2)	(107.5)	(109.4)	(143.3)	(57.8)	(72.6)	(174.6)	(117.4)	(44.7)	(44.6)

	Burn (BR)	Control (CT)	Mix (MX)	Mound (MD)	Scalp (SC)
Total	2105.6 (910.6) ab	1554.7 (654.4) ab	1188.6 (501.1) b	2308 (1217.5) b	2333.8 (902.6) a